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"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—JAMES SMITHSON

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LEONARD CARMICHAEL,
Secretary, Smithsonian Institution.

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EVOLUTION OF ARTHROPOD MECHANISMS

By

R. E. SNODGRASS

Research Associate of the Smithsonian Institution
Collaborator of the United States Department of Agriculture



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EVOLUTION OF ARTHROPOD MECHANISMS

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INTRODUCTION

Any study of evolution necessarily involves theories, but if we stopped short with known facts our phylogenetic trees would wither at the roots. Particularly when we attempt to reconstruct events that took place in remote Precambrian times we can have recourse only to our imagination. Where connecting links between modern animals cannot be known, we must invent them; at least, if evolution is true, we can feel sure that connecting links really did exist. Imagination, of course, must be controlled by reasoning from the known to the unknown, but unfortunately our brains do not all reason in the same way and often produce very different concepts from the same set of facts. Yet some ideas should be more plausible than others.

Though many zoologists hold that the arthropods have been evolved from polychaete annelids, the following discussions are based on the belief that the Polychaeta, having lateral swimming appendages, or parapodia, are a branch of the chaetopod annelids descended from some remote, simple segmented worm (fig. 1 A), and that the Onychophora and Arthropoda are derived from the same ancestral worm stock, but from forms that developed lateroventral lobelike appendages (B) and became crawling or walking animals. They presumably lived in shallow water where they crawled on the bottom, over rocks, or on water plants. The theoretical phylogenetic stage represented at B is literally reproduced in an early embryonic stage of the Onychophora, and is approximately recapitulated in the ontogeny of various arthropods. From their common lobopod ancestors the Onychophora and the Arthropoda diverged as two separate lines of descent, the onychophorans retaining a flexible integument, the arthropods acquiring a sclerotization of the cuticle, which allowed the legs to become longer (C), and finally jointed (D). The difference in the nature of the body wall thus accounts primarily for other differences in the organization of these two related groups of walking animals.

That the modern terrestrial Onychophora have descended from

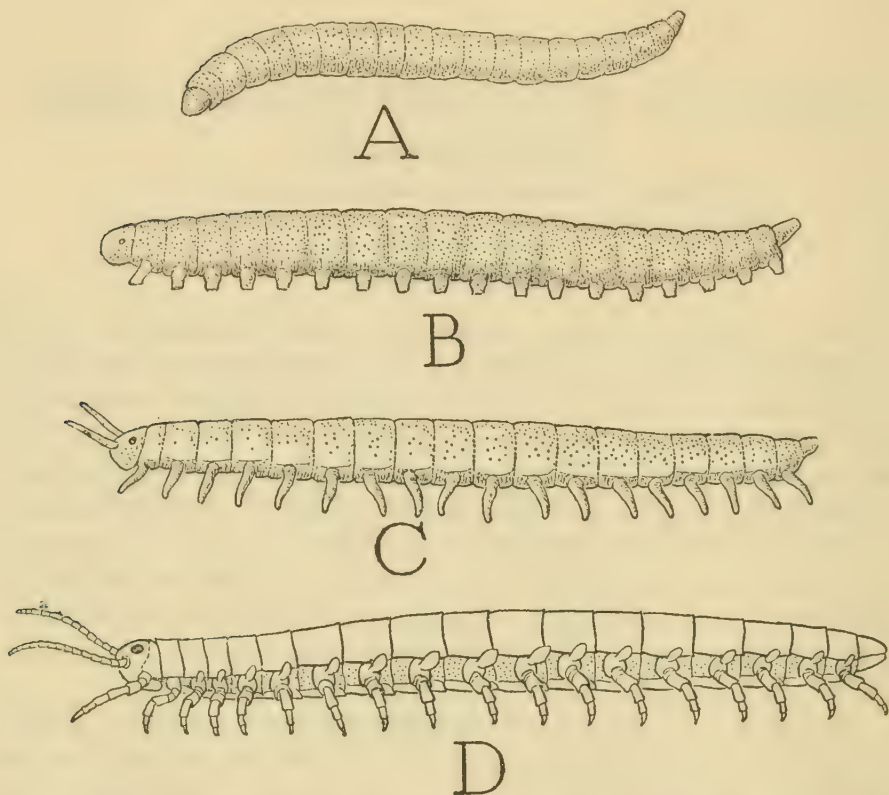


FIG. 1.—Theoretical evolutionary stages from a simple segmented worm to a primitive arthropod.

A, A primitive segmented Precambrian worm without bristles or appendages, from which may have been derived the chaetopods on one evolutionary line, and the lobopods on another. B, A crawling derivative of A with small lateroventral lobelike outgrowths of the segments (repeated in the embryogeny of Onychophora and all arthropods) from which might have been evolved directly the soft-skinned Onychophora. C, A walking form derived from B by sclerotization of the integument, allowing the limbs to become longer and slenderer. D, A primitive arthropod derived from C, with jointed appendages.

very ancient aquatic ancestors is attested by the presence of the genus *Aysheaia* in the middle Cambrian. There can be little doubt that *Aysheaia* (fig. 2 E) is an onychophoran, though it differs externally in some ways from any modern form. It has been depicted by Hutchinson (1931) as having a pair of branched appendages arising dorsally at the back of the head. An examination of the specimens in the U. S. National Museum, however, shows clearly that the branched appendages are the first pair of legs. In two specimens, including the type (D) described by Walcott (1911) as *Aysheaia pedunculata*, the

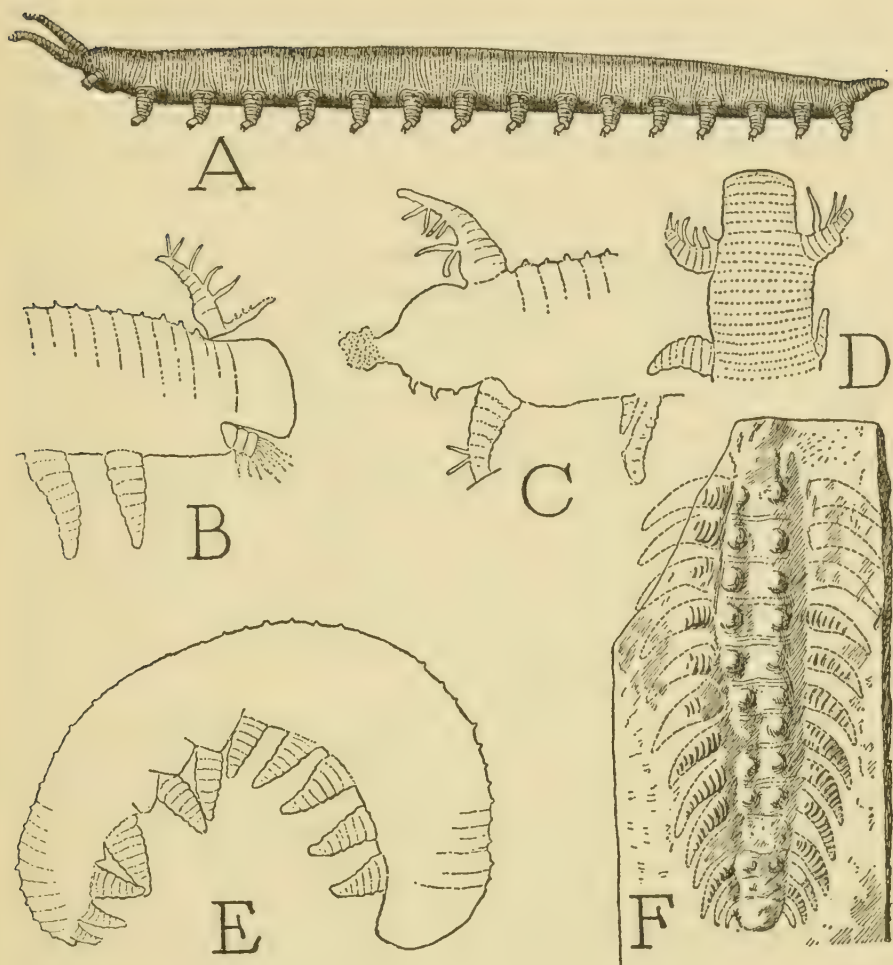


FIG. 2.—Onychophora, modern and ancient.

A, *Peripatoides novae-zealandiae*, modern. B, C, D, E, *Aysheaia pedunculata*, Cambrian (from specimens in U. S. Nat. Mus.). F, *Xenusion auerswaldae*, Algonkian (from Heymons, 1928).

branched first legs are spread out symmetrically on opposite sides. In the specimen studied by Hutchinson (B) one appendage is fully preserved and is dorsal, but it is evidently detached from the body of the animal and displaced dorsally; the other appears to be the stump of an annulated limb frayed out distally into irregular strands of an uncertain nature. On a fourth specimen (C), in which the anterior end of the body is twisted to the left and the head somewhat mashed, the first legs are extended laterally; the right one is fully branched, the left shows at least two small spikelike branches. All specimens suffi-

ciently well preserved show the presence of 11 pairs of legs, including the branched first legs. The general similarity of the head region of *Aysheaia* (E) to that of a modern onychophoran is suggestive that *Aysheaia* had a pair of concealed jaws. The specimens do not have a sufficiently primitive, or "embryonic," appearance to support Hutchinson's suggestion that the second pair of legs become the jaws of modern species.

The largest and best-preserved specimen of *Aysheaia* in the Museum collection (fig. 2 E) shows no branches on the front legs, though they might be concealed on the mesal surfaces; or perhaps there were different species of *Aysheaia*. The most striking difference between modern Onychophora and the Cambrian fossils is the entire lack of any remnant or trace of antennae on the head of the latter. Hutchinson suggested that the branched appendages, which he thought were dorsal, become the antennae in modern Onychophora, but the migration of these appendages to the front of the head seems very improbable. Walcott (1911), taking *Aysheaia* to be a polychaete, interpreted a very indistinct formation in the shale seen at the anterior end of the type specimen (but not shown at D) as a head and minute tentacles of the supposed worm.

Inasmuch as there is no evidence of the presence of antennae in the Cambrian Onychophora, it might appear that these appendages of modern forms are a more recent acquisition. Five hundred million years is a rather long time, and probably sufficient for the development of a pair of tentacular appendages from the front of the head, as well as a primitive tracheal system for life on land, considering what other animals have accomplished in the same time. Unfortunately there is no evidence as to the antiquity of the terrestrial onychophorans. In the other direction, *Aysheaia* is preceded by the Algonkian *Xenusion* (fig. 2 F), which, as figured by Heymons (1928), appears to belong to the onychophoran line of lobopod evolution. In any case, it seems that the Onychophora have given rise to nothing but forms of their own kind.

On the other hand, that the Onychophora and the Arthropoda are fundamentally related through some remote lobopod ancestor is attested by the following characters they have in common: (1) The lateroventral position of their appendages, which develop alike in the embryo from simple, lobelike outgrowths of the body wall; (2) the undivided body cavity (mixocoel) in the adult stage; (3) the presence of coelomic excretory organs with simple coelomic exit ducts; (4) a single pair of coelomic gonadial sacs, which in the arthropods may be branched, within which the germ cells are developed, and are

discharged through a pair of coelomic ducts, which may unite in a common ectodermal exit duct; (5) the origin of the nerve cords from "ventral organs" of the ectoderm, characteristic of the Onychophora and retained in Symphyla and Pauropoda among the arthropods. In one important respect the Onychophora differ from adult arthropods, namely, in the wide separation of the nerve cords.

The ancient onychophorans undoubtedly were aquatic, and their modern terrestrial descendants must still live in permanently damp places. The rate of water loss from the body of *Peripatopsis*, as determined by Manton and Ramsay (1937), is twice that of an earthworm and 80 times that of a cockroach. Water loss probably is due mainly to the large number of spiracles scattered over the body, which have no closing apparatus. The primitive open tracheal system alone, Manton and Ramsey suggest, may have been responsible for the onychophorans not becoming a widely spread or diversified group of modern animals. The Onychophora are poor relations of the arthropods, and not their ancestors.

The terrestrial arthropods having a sclerotized integument, and especially the insects with closing valves on their spiracles, have not been handicapped for living in dry environments. The contrast between the simple, soft-skinned onychophorans, and the structurally highly diversified, hard-shelled arthropods, however, has resulted largely from the ease with which skeletomuscular mechanisms can be evolved from a sclerotized integument on which the somatic muscles are attached. The modern arthropods, therefore, are noted for the number of anatomical tools and mechanisms they possess, and for the great variety of forms into which they have developed.

Students of evolution do not ordinarily consider the fact that with each new mechanical device an animal acquires, the animal must know how to use it. The animal's "know how" is instinctive, that is, automatic, and this presumably implies that a new sensory-motor system has been at the same time developed in the nervous system. The copulatory genital structures of insects, for example, are often highly complex, so complex that taxonomists who study them intensively for specific characters do not know in most cases how the insect uses them. The insect knows exactly how to use each part, but we at present know nothing of the nervous apparatus by which the mechanism is instinctively operated.

The problem becomes still more complicated where arthropods acquire different mechanisms in different stages of their life histories. The caterpillar or the larva of a fly or bee, for example, has a relatively simple feeding apparatus that responds to the stimulus of food, but the

adult acquires a very different kind of mechanism adapted to feeding in a different way on a different kind of food. The feeding apparatus of an adult bee is so complicated that understanding its physical structure requires a painstaking study on the part of the anatomist, but the bee operates this intricate mechanism without giving it a thought (since it can't think). During the transformation of the bee from the larva, therefore, there must have been developed in the feeding center of the nervous system a whole new complex of sensory and motor fibers, as well as new sense organs responsive to the stimulus of a new kind of food. The task of natural selection has then been a double one of bringing into correlation a skeletomuscular mechanism and a neural mechanism—if natural selection alone accounts for evolution.

The term "instinct" covers a vast field of ignorance. If automatic behavior has a specific structural basis in the nervous system, activated by sensory stimuli, a desideratum for the future is a treatise on "The Anatomy of Instinct."

I. ARTHROPOD INTERRELATIONSHIPS

Now that we have differentiated the arthropods from the onychophorans, after deriving both from a lobe-footed worm, something should be said about the relationships of the arthropods to one another. The theme is really not worth the space of a full discussion, since the subject is not one of known facts, and the connecting links are entirely missing. However, it will clarify some of the following discussions to give here a brief outline of the scheme of relationships adopted in this paper.

If we reduce the arthropods to a common plan of structure the primitive arthropod must have been an elongate, segmented animal (fig. 1 D), with a head represented by the cephalic lobe in a modern embryo, and a pair of jointed appendages on each body segment. The trilobites retained a primitive condition only in their limbs, which were all uniformly segmented walking legs. Otherwise, the trilobites in their body structure were already highly specialized by early Cambrian times. The Xiphosurida resemble the trilobites so much in the structure of the prosoma that they must have had a remote connection with the trilobite ancestors, but their prosomatic appendages are literally those of the arachnids, so evidently these latter two groups are somehow related. The Eurypterida, Xiphosurida, Pycnogonida, and Arachnida constitute the Chelicerata, so named because their principal feeding organs are the chelicerate first pair of postoral appendages; they have no true masticatory jaws, and lack antennae.

The rest of the arthropods, including the crustaceans, the myriapods, and the insects, are known as the Mandibulata because they have mandibles, but in other respects also they so consistently differ from the Chelicerata as to leave no doubt that the two groups represent distinct lines of arthropod evolution. Within the Mandibulata, however, the relationship of the component groups is obscure. The crustaceans are the earliest mandibulates known in the fossil record, but there is no evidence whatever yet found as to when or where the ancestral myriapods and insects originated. The crustaceans appear to be an independent branch of the mandibulate line; they are the only mandibulates that preserve functional second antennae and retain both the dorsal and the ventral muscle of the dactylopodite.

The myriapods and the insects are themselves distinct groups, but they have in common enough characters to separate them as a group from the Crustacea. They lack second antennae, except as embryonic vestiges, and they consistently lack the dorsal (levator) muscle of the pretarsus (dactylopodite). A centipede in its general form and number of unmodified legs might appear to be closest to a primitive arthropod, but nothing is known of its ancestry. It has been argued that the insects were derived from crustaceans, but their affinities with the myriapods, perhaps through symphylan progenitors, is too close to allow them an independent status. The evidence of relationship of the insects to the myriapods rather than with the Crustacea has been well discussed by Tiegs (1949). Remington (1955) also contends that the available evidence leads to the conclusion that the myriapods and hexapods are a series of forms with a common ancestor. Some writers have proposed a separate origin of the myriapods from primitive Onychophora, but the mandibulate arthropods are too evidently a monophyletic group not to have had a single origin.

Though it is to be assumed that all the arthropods came from aquatic stock, we have no evidence as to how or when the terrestrial myriapods and insects came out of the water. It has been suggested by Ghilarov (1956) that the primitive insects on leaving the water penetrated the earth along the shore and were at first soil dwellers. The same even more probably might have been true of the myriapods. In this case, the transition from water to air would have been less abrupt, though still it was necessary to develop a tracheal respiratory system before life on dry land could be practical.

The myriapods differ from the insects in having seven segments in the legs, the insects having only six. The insect mandible maintains a unit structure whatever form it may take. In the chilopods the gnathal

lobe is flexible on the mandibular base; in the diplopods and symphylans the lobe itself becomes the functional jaw independently movable on the base of the mandible. The diplopods are the most specialized of the myriapods. The insects owe their body structure first to having become hexapods through the elimination of all body appendages except the first three pairs, next to the specialization of the thorax as the locomotor center of the body, and finally to the development of wings. With the acquisition of organs of flight they left their crawling relatives behind and assumed the leading role in arthropod evolution. They have overpopulated the earth with their progeny, who have come into competition with the descendants of *Homo sapiens*, and have thereby raised the profession of entomology to a high rank.

II. BODY SEGMENTATION

Body segmentation, or metamerism, is characteristic of the Annelida and the Arthropoda, and is an adaptation to body movement, but the segmental mechanism is not the same in these two groups of segmented animals. The Onychophora also are fundamentally segmented, though in the adult stage the segmentation of the body wall is suppressed; their body mechanism again differs from both that of the annelids and that of the arthropods.

The phylogenetic origin of metamerism is usually deduced theoretically from embryonic development, because the embryo has been said to repeat the history of its race. An embryo shut up in an egg, however, lives under conditions that are very different from those of its free-living ancestors, and for this reason its developmental story cannot be taken too literally as a repetition of its adult race history. It is confusing also to find that embryos of related species often differ much in their methods of development, and arrive at the same end results in quite different ways. Moreover, the embryo may develop into a highly metamorphosed larva adapted to a different way of living from that of its parents. In such cases the larval form and structure may be in no sense ancestral, and the larva must undergo a second metamorphic transformation to get back into the adult form of its species.

The embryonic origin of body segmentation is much better shown in the polychaete annelids and the Onychophora than in the development of the arthropods and may be taken to repeat more nearly the origin of segmentation in the ancestors of these three groups. The polychaete larva, known as a trochophore, is a minute top-shaped

creature designed for floating upright in the water and for swimming by means of circles of vibratile cilia in order to distribute the members of its species before they take on the worm form and habits. The trochophore, therefore, has to undergo a metamorphosis to become a worm, and neither the trochophore itself nor its metamorphosis recapitulates anything in the history of its adult ancestors, any more than does the caterpillar and its change into a butterfly represent anything in the adult history of the Lepidoptera. The trochophore becomes a worm through elongation of its postoral part by teloblastic generation of new tissues in a subterminal zone of growth. The newly formed body becomes segmented as coelomic cavities are formed in its mesoderm bands, but the way segments are formed by growth from the rear end of the body is a metamorphic process.

We had better turn to the Onychophora then for a more reliable picture of the primitive beginning of body segmentation. The Onychophora have no differentiated larval stage; the embryo in the egg develops directly into a miniature segmented adult, and its early embryogeny has been fully described by Manton (1949) and others. The mesoderm grows forward from the region of the blastopore as two lateral bands that extend to the mouth. The bands then become divided from before backward into solid blocks, which immediately are excavated by coelomic cavities. The first cavities converge in front of the mouth and become the coelomic cavities of the antennal region.

Most embryologists call the coelomic sacs "the somites," but the term *somite* should be synonymous with "body segment." However, the segmentation of the mesoderm is unquestionably preliminary to body segmentation, since, Manton says, there is no ectodermal segmentation until after the mesodermal somites are completed. The outer walls of the coelomic sacs in the annelids, onychophorans, and arthropods give rise to the somatic muscles, and it is the muscles that mechanize the body for locomotion and make the segments functional motor units, except where external segmentation is later suppressed as in the Onychophora. It might thus appear that the whole future organization of the segmented animal is determined by the formation of two rows of holes in the mesoderm. However, in evolution structures do not arise for what they may later become, and hence there must have been some independent functional reason for the first formation of the mesodermal cavities, the presence of which in itself can hardly be regarded as a segmentation of the body. Two principal theories have been proposed to explain the origin of the coelomic cavities, one is the *nephrocoele* theory, the other the *gonocoele* theory,

but neither need concern us here in a study of the later-developed skeletomuscular mechanisms that owe their inception to the coelomic sacs.

The somatic musculature of the annelids consists of an outer layer of circular fibers and an inner layer or bands of longitudinal fibers. In their origin the longitudinal muscles are said to be perfectly metameric, but later their metamerism is entirely effaced (Dawydoff, 1928). In the adult of *Nereis* or an earthworm these muscles are composed of fine, threadlike fibers that are continuous through the segments. The fiber bundles of *Nereis* are bound to the body wall at the intersegmental grooves, but the fibers have no attachment on the cuticle. In the earthworm the longitudinal fibers form a layer surrounding the entire body cavity, except along the middorsal line and at the insertions of the setae; they have no attachments on the body wall. The parapodia of the polychaetes have their own muscles arising on the body wall.

The locomotor movements of *Nereis*, as analyzed by Gray (1939), are very complex whether for crawling on the ground or for swimming, and involve coordinated action of both the body musculature and the muscles of the parapodia. The locomotor mechanism of the earthworm is more simple. As shown by Chapman (1950) it is the antagonistic action of the circular and longitudinal somatic muscles on a fluid-filled body that gives the earthworm its principal means of locomotion by contracting the rear part of the body and pushing out the front.

The onychophoran body musculature is highly complex; it covers the whole inner surface of the body wall, and the fibers have no segmental attachments. It includes an external layer of circular muscles, a double layer of oblique fibers crossing in opposite directions, dorso-ventral lateral fibers, and bands of internal longitudinal fibers. Unlike the worms, the onychophoran is a walking animal; its legs have a strong extrinsic and intrinsic musculature. The body is a relatively rigid cylinder and takes no part in the progressive movement of locomotion. As observed by Manton (1950), however, "the movements of *Peripatus* are much more varied than they are in terrestrial Arthropoda provided with an exoskeleton." The head end of the body anterior to the second or third pair of legs is turned to right or left as the animal goes forward, and "the head and antennae may be raised and lowered with an irregular rhythm."

When we turn to the arthropods we encounter an entirely different kind of mechanical organization from that of either the Annelida or

the Onychophora. Of prime importance is the sclerotization of the arthropod cuticle; second, the direct attachment of the somatic muscles on the cuticle by means of cuticular tonofibrillae; and third, the breaking up of the longitudinal muscle fibers into bundles of segmental length. The general plan of the arthropod body musculature is much simplified as compared with that of an onychophoran. It consists essentially of dorsal and ventral bands of longitudinal fibers, and dorsoventral lateral muscles, which latter perhaps are remnants of primitive circular muscles. In contrast to the reduction of the body musculature, there is a strongly developed musculature of the appendages, befitting a walking animal. As Manton (1950) has noted, "a reduction of the propulsive force provided by the longitudinal body muscles and an increase in that supplied by the extrinsic muscles of the limbs must have been an important step in the evolution of limbs for terrestrial locomotion." The same, of course, might be said of adaptation to locomotion by legs in an aquatic environment. The first arthropods were inhabitants of the water and had fully developed legs (as the trilobites), but having learned to walk under water, it was a simple matter for some of their descendants to walk on land.

The principal longitudinal muscles of the arthropods, except where segments are united or otherwise modified, are firmly attached to the cuticle on the primary intersegmental grooves, which are sclerotized to form anterior marginal or submarginal internal ridges (antecostae) on the tergal and sternal plates. There are, therefore, no true intersegmental lines of movement in the skeleton, and this condition involves another essential modification of the body wall to allow the segmental plates to be movable on each other. The so-called "intersegmental" membranes are not intersegmental; they are the unsclerotized posterior parts of the primary segments. The functional "segments," or the segmental plates, are merely the sclerotized parts of the primary segments, including the intersegmental ridges, or antecostae, on or near their anterior margins. The functional segmentation of the arthropod, therefore, is a secondary segmentation, and does not correspond with the polychaete segmentation defined by the flexible primary intersegmental grooves. Without this adaptation in the arthropod skeleton, a wholly sclerotized integument would encase the animal in an inflexible tube.

While it is probable that body segmentation of the Annelida, Onychophora, and Arthropoda had its origin in some simple wormlike common ancestor, the locomotor mechanism has been differently developed in each group. The arthropods attained the most efficient mechanical organization, but considering the many essential adaptive

modifications of structure that were necessary, it is evident that the transformation of a simple segmented worm into an arthropod involved a long and complex evolutionary process. Once the arthropods attained the essential features of their organization, however, they were endowed with unlimited possibilities for further development and differentiation.

III. SCLEROTIZATION AND SCLERITES

The primitive cuticle of the annulate animals was probably a proteinaceous product of the epidermis; in modern arthropods and onychophorans it is more or less impregnated with chitin. The cuticle of most adult arthropods is hardened, or sclerotized, in definite areas to form *sclerites*.

Typically the arthropod cuticle consists of two principal layers, a thicker, inner chitin-containing layer, the *procuticle* of Richards (1951), and a very thin, nonchitinous surface layer, or *epicuticle*. Cuticular sclerotization among the arthropods in general may result either from the deposit of calcium salts in the inner part of the cuticle, or from a hardening of the protein constituent. Calcium sclerotization occurs principally in the Crustacea and Diplopoda, probably in combination with protein sclerotization; protein sclerotization is characteristic of the insects. Sclerotization of the insect cuticle, when present, affects the epicuticle and the outer part of the procuticle, differentiating the latter into an outer dense *exocuticle* and a softer, inner *endocuticle*. The protein sclerotization in the insect cuticle, as described in a recent review by Wigglesworth (1957), is a very complex chemical process. As deduced from a study of fly puparia (see Richards, 1951), there is first an oxidase given off from the blood through the epidermis that penetrates the cuticle into the epicuticle. Then tyrosine, or some oxidative product of it in the blood, goes through the epidermis and the procuticle and is tanned by the oxidase in the epicuticle to an O-quinone, which then diffuses inward and tans the outer part of the procuticle into a hard exocuticular layer. The endocuticle appears to be immune to the tanning process.

The remarkable feature about cuticular sclerotization is that it results in the formation of definitely limited *sclerites* separated by non-sclerotized areas of the cuticle, commonly called membranes. If the sclerotizing elements come from the blood, it is difficult to understand why they do not penetrate the entire cuticle. The pattern of sclerotization is distinctive of species, and must be determined by hereditary factors. The various sclerotic patterns, moreover, are intimately

adapted to the skeletal mechanism of the animal. Evidently there must be some preliminary differentiation in the epidermis that determines the pattern of sclerotization.

Though the sclerites in general have definite limits, sclerotization may be continuous from one part of a segment to another, as in insects where the pleural and ventral sclerotization of a thoracic segment may not be separated. In such cases it is often assumed that the pleuron has extended ventrally and crowded out the sternum. If there is truly a replacement of the skeleton of one body region by extension from that of another, there should be a corresponding extension of the epidermis. Otherwise, the condition of sclerotic continuity may be merely a confluence of sclerotization, as when an entire segment becomes a continuously sclerotized annulus.

Then finally, there is the question of how it came about in the first place that sclerites were laid down in conformity with the mechanical needs of the animal. Was sclerotization at first a haphazard process, from which proper sclerites were evolved by trial and error, with errors eliminated by natural selection, until the animal became a working mechanism? If so the arthropods must have had a hard time getting a practical start. Unfortunately the fossil record gives us no information on the early evolutionary stages of the arthropods, when they might be called "Proarthropoda."

It is clear that arthropod sclerites are in no way equivalent to the bones of a vertebrate animal. Primitive sclerotized areas can be broken up into smaller parts or fused into a larger unit. On the other hand, secondary desclerotization often occurs, as in the abdomen of a hermit crab. Leg segments can be eliminated, or divided into sub-segments. The vertebrate animal is limited by its bones to a certain form; the skeleton has little plasticity, except for the increase of vertebrae and ribs or the reduction and loss of appendages. The difference between a man and a snake is insignificant compared with that between a crab and a *Sacculina* parasitic within it.

IV. SCLEROTIZATION OF THE BODY SEGMENTS

The body segments of an annelid worm without appendages are mere integumental rings limited by circular grooves. In an animal having lateroventral appendages (fig. 3 A), however, the periphery of a segment is divided into a *dorsum* (*D*) above the limb bases, and a *venter* (*V*) between them. It is with the development of sclerotization that complexities arise in the segment structure, since the pattern of sclerotization may be very different in different arthropods, or even on different body segments in any one species.

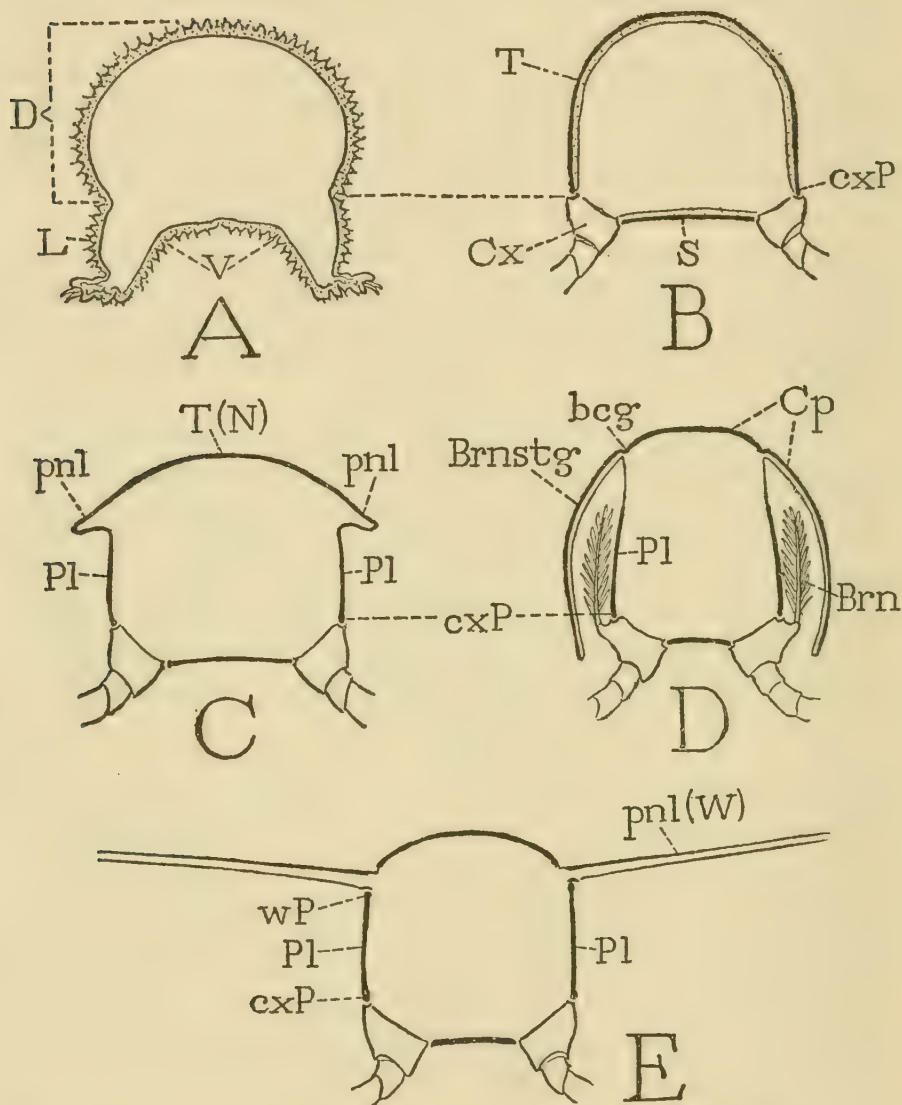


FIG. 3.—Diagrammatic cross sections of body segments, showing differentiation of surface areas.

A, Cuticle unsclerotized. B, Sclerotization forms a tergal and a sternal plate. C, Dorsal sclerotization differentiated into tergum, or notum, and pleura by paranotal lobes. D, Tergum replaced by a carapace (*Cp*) produced into gill covers (*Brnstg*), pleural areas become inner walls of gill chambers. E, Paranotal lobes produced into wings.

Though there can be no doubt that integumental sclerotization is the basis of modern arthropod structure and mechanisms, we have no evidence as to the pattern it first assumed. It seems reasonable that sclerotization was primarily developed for protection, but it is improbable that the body segments of a soft-skinned wormlike ancestral form became at once hard rings. Perhaps there was first formed in each segment a tergal plate on the back and a sternal plate on the venter, leaving the lateral areas soft and flexible. With such a structure the early arthropods could preserve something of the hydraulic motor mechanism of their vermiform progenitors, which is still operative in some soft-skinned larvae. With the development of limbs, however, body movements became less important in locomotion, and in most adult modern arthropods the side walls of the segments are sclerotized to support the appendages.

When we turn to modern arthropods, it is only a matter of opinion as to which retain a primitive type of sclerotization, and which are specialized. Among the crustaceans and diplopods the entire dorsum of a segment may be continuously sclerotized (fig. 3 B), in which case the name tergum (*T*) must apply to the whole back plate. In the crustacean *Anaspides* (fig. 4 B), for example, the dorsal plates of the thoracic segments continue down on the sides and support the legs on their lower ends, though each is cut by a slight groove near the lower margin that demarks a small laterotergite (*ltg*). A similar condition is shown in a cross section of the head of an insect (*A*), in which the mouth parts are suspended directly from the ventral edges of the cranial walls. Likewise in malacostracan crustaceans in which the carapace is short or attached on only a few thoracic segments, as in Mysidacea (fig. 6 B, C), Cumacea, and Stomatopoda, the terga of the free segments are simple dorsal arcs carrying the legs on their lower margins (*G*). In all these forms there is no anatomical distinction between tergum and pleura.

The legs of an isopod (fig. 5) are suspended from lateral lobes or plates (*Cx*) of the dorsal walls of the thoracic segments. These plates, usually called "epimera" by carcinologists, look like laterotergites, but according to Gruner (1954) they are formed in the embryo from the coxae of the legs; in some forms, as in *Porcellio* (*A*), they have become continuous with the terga. Corresponding plates in the amphipods (fig. 13 D, *Lcx*) are freely suspended from the tergal margins. If these plates on the leg bases are truly coxal, there is no part of the skeleton in the isopods and amphipods intervening between the terga and the coxae that can be regarded as pleural; the legs are here again carried directly on the tergal margins.

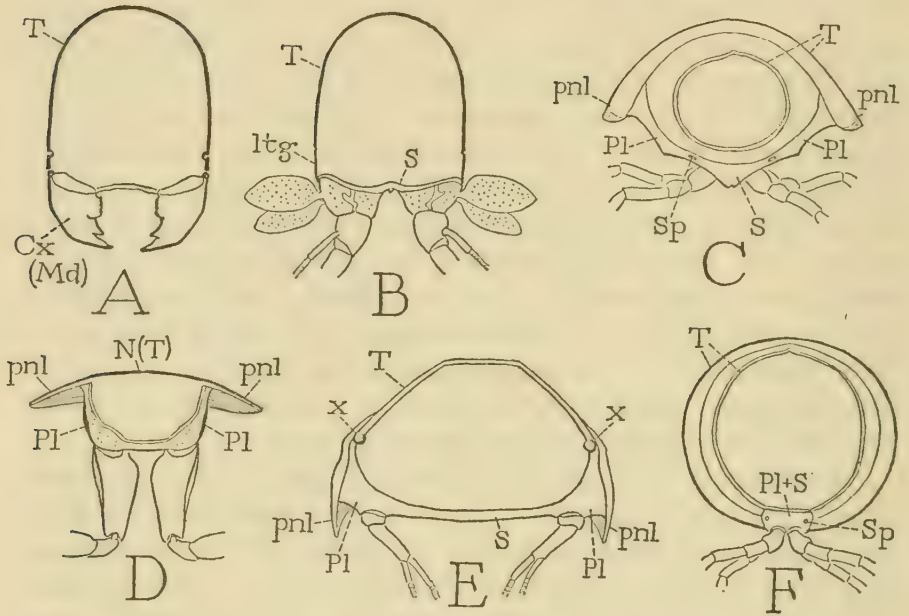


FIG. 4.—Examples of segment modifications.

A, Vertical section of head of an orthopteroid insect. B, Vertical section of thoracic segment of crustacean *Anaspides*. C, Segment of a polydesmoid diplopod, anterior. D, Prothorax of a cockroach, *Periplaneta*, posterior. E, Abdominal segment of female crayfish, anterior. F, Segment of a juliform diplopod, anterior.

x, x, articular condyles.

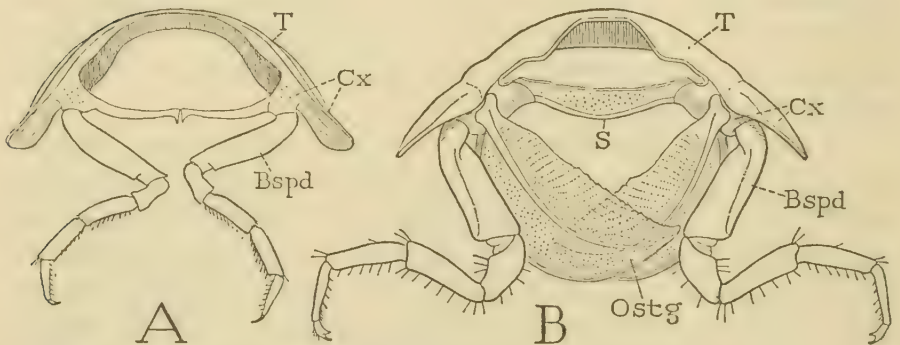


FIG. 5.—Thoracic segments of isopods.

A, *Porcellio lacvis*, male, anterior. B, *Ligyda exotica*, female, posterior.

Where the dorsum of a segment is continuously sclerotized, it is only when some structural feature, such as paranotal lobes (fig. 3 C, *pnl*), separates the back from the sides of the segment that we arbitrarily restrict the term tergum (*T*) to the back, and call the lateral areas below the lobes *pleura* (*Pl*). Thus in a polydesmoid diplopod (fig. 4 C) or the abdomen of a decapod (E), in which the segments are wholly sclerotized annuli, the lateral areas between the paranotal lobes and the limb bases are conventionally designated *pleura* (*Pl*). In the cylindrical juliform diplopods, which have no paranotal lobes, each tergum (*F*, *T*) is continued downward on the sides to a small ventral plate (*Pl+S*) that contains the spiracles (*Sp*) and supports the legs. Since the spiracles of the polydesmoid are in the pleural areas, the ventral plate of the julid is evidently a pleurosternum, in which the pleural components are greatly reduced and separated from the tergum. The wings of insects (fig. 3 E) appear to have been evolved by a great extension of paranotal lobes; the lateral areas below them by definition are pleural (fig. 3 E).

It might be supposed that the gill covers, or branchiostegites, of the decapod crustaceans (fig. 3 D, *Brnstg*) are structures analogous to insect wings developed from paranotal lobes of the thoracic terga. The decapod structure as seen in cross section, however, is misleading. The carapace is *not* the united terga of the segments it covers; it is a posterior fold from the maxillary region of the "head shield," which has extended through the thoracic dorsum as far as the last segment and replaced the median parts of the invaded terga. The branchiostegites are lateral folds of the carapace.

A halfway stage in the replacement of the thoracic terga by the maxillary carapace is well shown in the Mysidacea, in which only three or four thoracic segments have been invaded by the carapace, though the latter may cover the entire thorax (fig. 6 A). When the carapace is removed from the thorax there is exposed a large V-shaped hole in the dorsum of the first three segments (B, C), on the margins of which is attached the inner lamella of the carapace. The dorsal parts of the thoracic terga in this region have been obliterated by the invasion of the carapace, and the lateral parts have been pushed back dorsally and drawn out into tapering tongues converging toward the end of the carapace attachment. In the decapods then, the attachment of the carapace has been extended from the maxillary region through the first seven thoracic segments, and has completely replaced the true tergal wall of these segments between the branchiocardiac grooves (fig. 3 D, *bcg*).

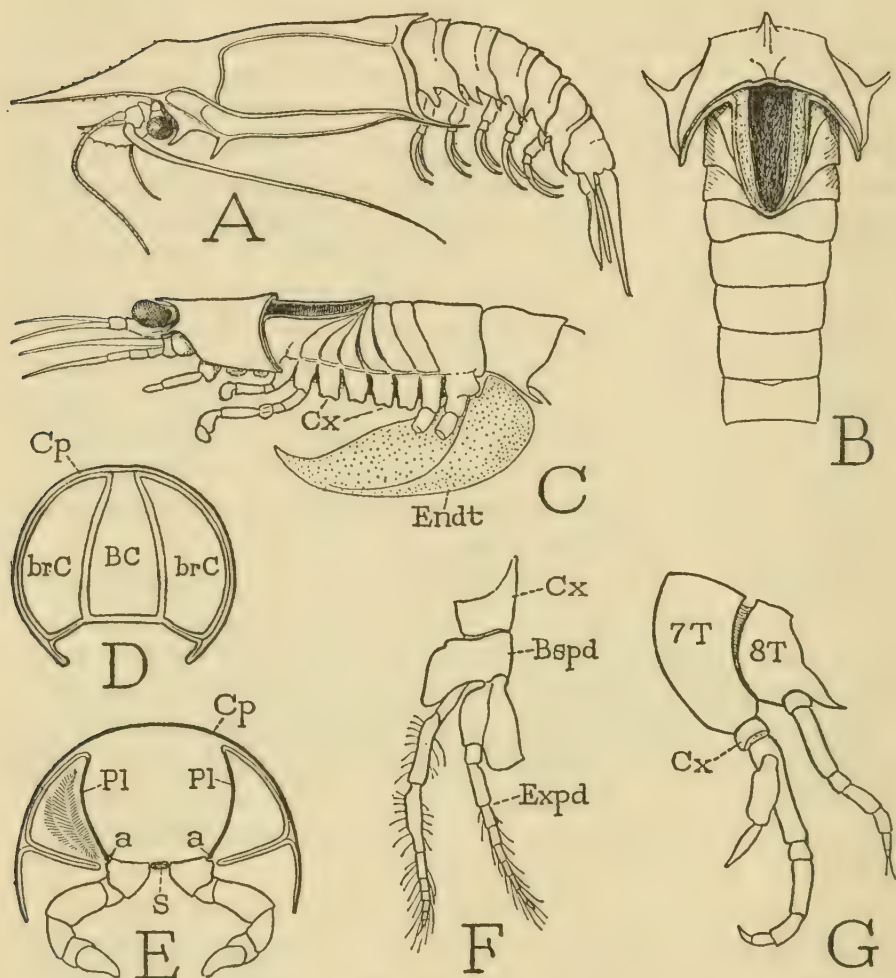


FIG. 6.—Formation of malacostracan carapace by extension from maxillary region, with conversion of lateral tergal areas of invaded segments into so-called epimeral, or pleural, plates carrying the legs.

A, *Gnathophausia calcarata bengalensis*, Mysidacea. B, Same, carapace cut off anteriorly, exposing its attachment by under lamella on back of thorax. C, *Acanthomysis dyboskii*, Mysidacea, carapace cut off behind maxillary segment, showing attachment on anterior thoracic segments. D, *Diastylis glabra*, Cumacea, section of second thoracic segment. E, *Emerita talpoida*, Decapoda, section of thoracic segment. F, *Acanthomysis dyboskii*, thoracic leg. G, *Diastylis glabra*, last two thoracic segments, showing direct suspension of legs from the terga.

The carapace of Cumacea commonly covers the first three, but sometimes more, of the thoracic segments. In *Diastylis* the carapace is attached by its inner lamella along only a narrow median strip of the back (fig. 6 D). Ventrally its wide lateral wings are connected by median submarginal flanges with the lower edges of the lateral body walls. The voluminous branchial chambers (*brC*) are thus entirely closed except anteriorly where the huge gill-bearing epipodites of the first maxillipeds project backward within them. The very short carapace of the stomatopods, likewise a fold from the maxillary segment, covers four of the thoracic segments, but it is attached on the back of only the first two segments, and the terga of these segments are cut by the carapace into lateral plates.

The malacostracan carapace is thus seen to be equivalent to that of the Notostraca and of *Nebalia*; but, instead of extending as a free fold over the thorax from the maxillary segment, it has united by its under lamella with the back of a varying number of thoracic segments, and has replaced the dorsal parts of their terga.

As an inference from the fact that the malacostracan carapace cuts through the back of the thoracic terga, it is clear that the plates on the inner walls of the gill chambers, still carrying the legs, though commonly termed "pleura" or "epimera," are actually the lateral parts of the severed terga. The concept that these plates represent "sub-coxal" segments of the legs, therefore, has no foundation in crustacean anatomy. That the so-called pleural plates are tergal remnants is confirmed on finding that in the decapods there are no dorsal muscles of the thoracic limbs or longitudinal body muscles attached on the back behind the second maxillary segment. All these muscles retain their primitive tergal attachments on the "pleura." (See Schmidt, 1915; Berkeley, 1928; Cochran, 1935).

In contrast to the condition found among the Diplopoda and in those Crustacea that have free thoracic segments, in which the pleural areas of the segments are sclerotized in continuity with the back, the pleural regions of the leg-bearing segments in various other arthropods may be largely membranous, or occupied by discrete pleural plates. In *Limulus*, for example, the wide membranous pleural regions of the prosoma contain only small Y-shaped sclerites on which the legs are articulated. In the Arachnida integumental folds between the carapace and the leg bases are all that can be regarded as pleural. The thoracic pleurites of apterygote hexapods are two small sclerites in the otherwise membranous pleural wall concentrically arched over the coxae (fig. 9 A, B, C). The thoracic pleural plates of pterygote

insects are always separate from the notum, but may be continuous with the sternum by precoxal or postcoxal bridges; they carry the legs and on the alate segments support the wings. In the chilopods the pleural areas of the segments are variously sclerotized, but the principal sclerites are closely associated with the coxae of the legs (fig. 8 H, K).

A very unusual pleural structure occurs among the diplopods in the Oniscomorpha. Two small spiracle-bearing plates on each side of the venter of each double segment (fig. 7 B, *pl*) intervene between the legs and a broad lateral lobe (*ltg*) inflected mesally from the lower

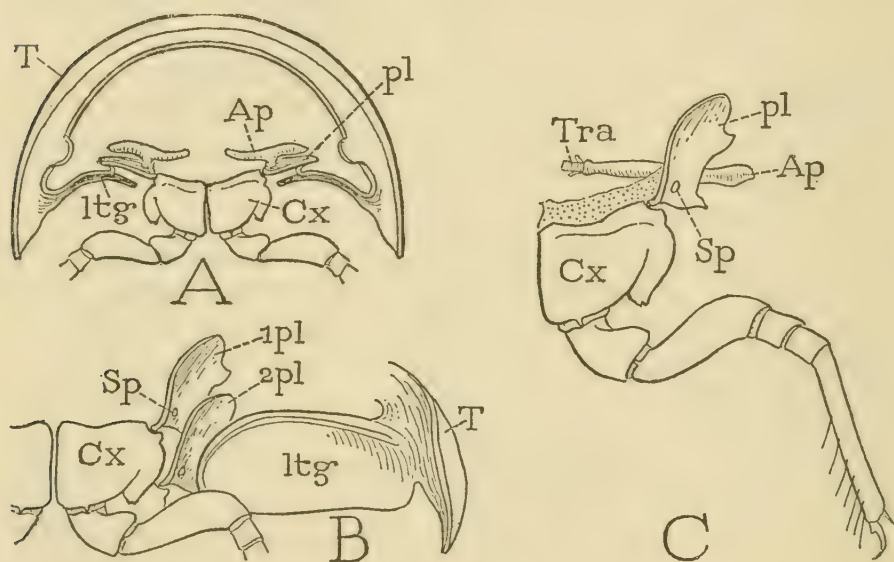


FIG. 7.—*Sphaeropoeus* sp., oniscomorph diplopod.

A, Section of body segment with leg attachments. B, Ventral view of left half of a segment, showing base of anterior leg, spiracle-bearing pleurites (*pl*), and laterotergite (*ltg*). C, A left leg, showing articulation on pleurite, and spiracular apodeme (*Ap*).

margin of the tergum. Inasmuch as the coxae articulate by their lateral basal angles on these spiracle plates (B, C) the latter can hardly be anything other than pleural sclerites, and the fact that they contain the spiracles is in harmony with the pleural position of the spiracles in the Polydesmoidea (fig. 4 C). The plates are termed "laminae pedigeræ" by Silvestri (1903) and "Stigmenplatten" by Gruner (1953), but Manton (1954) calls them "sternites." A true segmental sternum should lie between the coxae, but in the Oniscomorpha the coxae of each pair of legs are contiguous (fig. 7 A) leaving no space for a sternal sclerotization between them. In

Sphaeropocus the thickened mesal margins of the spiracle plates stand out as free folds, so that successive plates overlap each other (B). Laterally each plate is connected by membrane with the lobe (A, *ltg*) inflected from the tergum. While there are two pairs of spiracle plates for each double segment, there is only one pair of lateral tergal lobes.

According to a rather widely accepted theory, the pleural plates have been derived from the leg bases and represent primitive "subcoxal," or "precoxal," segments of the limbs. As already shown, the theory receives no support from the diplopods or crustaceans; the alleged evidence in its favor has been deduced principally from a study of the chilopods and insects.

In the chilopod *Scutigera* the lateral areas of the anterior body segments contain each a large supracoxal plate (fig. 8 H, *Scx*) marked by a median spiny ridge and scarcely separated from the coxa (*Cx*). On the posterior segments these plates are successively smaller (I), until on the last segment (J) the remnant of the plate is fully united with the coxa in a single basal segment of the leg. In a geophilid (K) a circular fold (*Scx*) completely surrounds the base of the much reduced coxa (*Cx*), and, though it is not completely sclerotized, it might well be imagined to be a basal segment of the leg. Yet here again, on the last body segment there is only a single basal plate supporting the rest of the leg. The supracoxal pleural plates of the chilopods, therefore, are evidently secondary derivatives of the coxae, and there is no evidence that they represent basal segments of the legs. In *Scutigera* they carry with them some of the body muscles of the coxae.

The pleural sclerites of some insect larvae lie in ventrolateral lobes of the thoracic segments (fig. 8 F, G), but nothing in the development of the larva suggests that these lobes are basal segments of the legs. Eventually the small pleural sclerites of the larva expand upward to form the pleural plates of the adult.

A subcoxal origin of the thoracic pleura of insects has been claimed by Heymons (1899) and by Roonwal (1937, 1939) to be shown in the embryonic development of Hemiptera and Acrididae. According to Heymons the primary basal segment of the embryonic leg in Hemiptera divides into a proximal subcoxa and a distal coxa. The subcoxa flattens out and forms the part of the thoracic wall on which the definitive leg articulates, and from which leg muscles arise. In the embryo of *Locusta*, as described by Roonwal, the primary leg bases divide each into a subcoxal segment (fig. 8 A, *Scx*), and a coxotrochanteral segment (*Cx+Tr*) that later separates into coxa

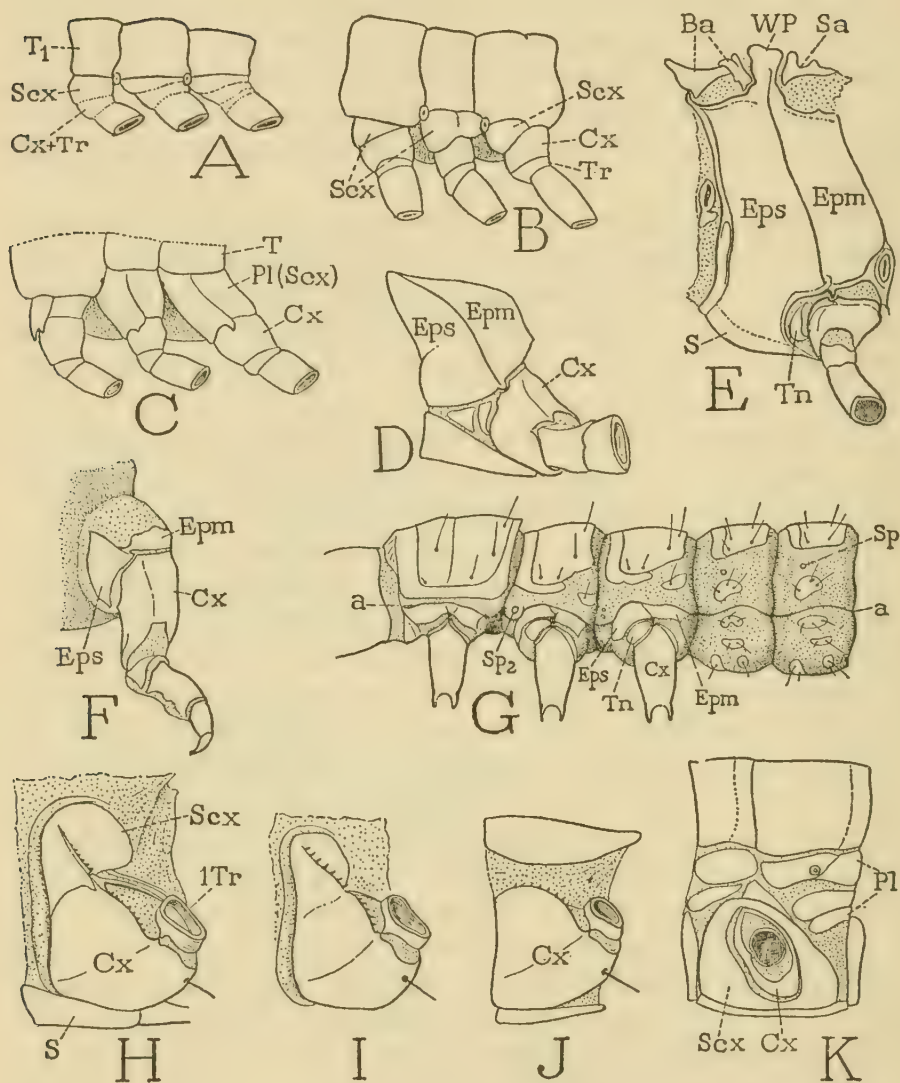


FIG. 8.—Features that have been interpreted as evidence of a subcoxal origin of the pleural plates. (A, B, C from Roonwal, 1937.)

A, Thorax and leg bases of young embryo of *Locusta*. B, Same, later stage. C, Same, newly hatched nymph. D, *Acheta assimilis*, mesothoracic pleuron and leg base of young nymph. E, *Dissosteira carolina*, mesopleuron and leg base of adult. F, *Pteronidia ribesii*, pleural sclerites and leg of larva. G, *Scarites* sp., carabid beetle larva, thorax and part of abdomen. H, *Scutigera* sp., centipede, leg base and "subcoxal" plate of eleventh leg-bearing segment. I, Same, thirteenth leg-bearing segment. J, Same, last leg-bearing segment. K, *Strigamia bothriopa*, geophilid centipede, middle body segment and leg base.

a-a, dorso-pleural line

and trochanter (B). The subcoxae then expand upward and become the pleura of the adult (C, *Pl*).

This evidence of subcoxal origin of the pleural plates as presented by Heymons and by Roonwal does not necessarily, as Heymons admits, substantiate the idea that the subcoxal elements were once the functional basal segments of the legs, though Heymons contends that the embryological evidence is in favor of the theory. However, since in isopods, amphipods, and chilopods plates in a pleural position are evidently formed from the coxae, it is quite possible that a mistaken significance may be given to the observed facts of embryonic development. The development of arthropod limbs in general gives little support to the theory of the derivation of the pleural sclerotization from a subcoxal leg segment.

The pleural sclerotization of a wing-bearing thoracic segment of adult insects generally covers most of the side wall of the segment (fig. 8 E). Characteristically it is marked by a median vertical or inclined groove that forms internally a strengthening ridge from the coxa to the wing, ending below in a coxal articular process, and above in a fulcral arm (*WP*) that supports the base of the wing. The pleural areas respectively before and behind the coxo-alar sulcus are the so-called *episternum* (*Eps*) and *epimeron* (*Epm*). Detached from the lower end of the episternum is usually a precoxal *trochantin* (*Tn*), which makes a secondary anterior articulation with the coxa. One or two *basalar* sclerites (*Ba*) lie in the subalar membrane before the wing fulcrum, and behind the latter is a subalar sclerite (*Sa*). These epipleural sclerites have an important function in the movement of the wing. A thoracic pleuron of this type is clearly constructed primarily for giving a strong support for the leg, and secondarily has been modified in the alate segments in adaptation to its relation to the wing and wing movements. The pleuron of the wingless prothorax, or that of a prospective alate segment of the nymph (fig. 8 D) or larva (F, G) bears a coxal articular process, but lacks the special features related to the wing.

The pleural sclerotization of the thorax in adult insects, however, undergoes various modifications in the different orders, and may be broken up into subsidiary parts, or reduced where the wings are small or suppressed. In a male scale insect, in which the hind wings have been reduced to a pair of small halterlike appendages, the metathoracic pleura, as shown by Ezzat (1956), are slender rods extending from the halteres to the coxae.

When we turn from the pterygote insects to the apterygotes we

find an entirely different type of sclerotization in the thoracic pleural regions (fig. 9 A, B, C). The pleural areas are here largely membranous, but in each segment are two narrow sclerites concentrically arched over the base of the coxa, a dorsal *anapleurite* (*Apl*) and a ventral *catapleurite* (*Cpl*). In the Lepismatidae (C) a third sclerite intervenes between the catapleurite and the coxa, which some writers regard as a trochantin, but it has the appearance of a basicoxite. Though the apterygote Protura, Collembola, and Diplura have no close relation to the rest of the hexapods, the Thysanura undoubtedly

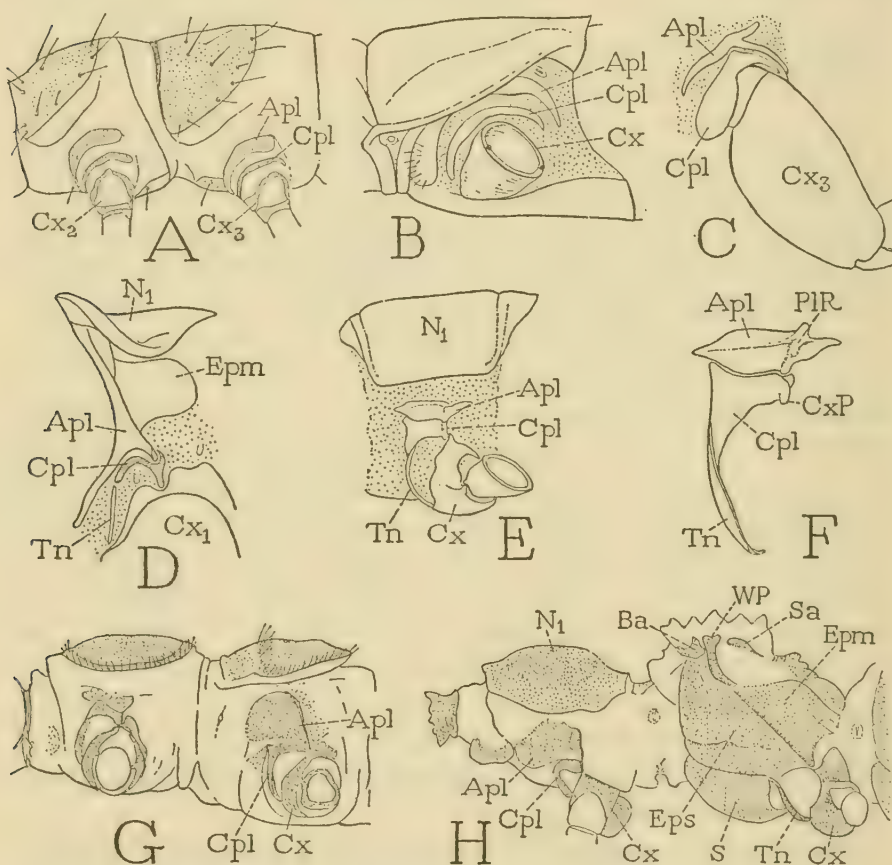


FIG. 9.—Thoracic pleura of insects: apterygotes, termite, and stonefly.

A, *Acerentomon doderoi*, mesothorax and metathorax (from Berlese, 1910). B, *Heterojapyx gallardi*, metathorax. C, *Ctenolepisma urbana*, metathoracic pleurites and coxa. D, Prothoracic pleuron of a winged termite (from Fuller, 1924). E, *Perla* sp., larva, prothorax. F, Same, right propleuron, internal. G, *Chloroperla grammatica*, prothorax and mesothorax of larva (from Grandi, 1950). H, *Protonemura* sp., prothorax and mesothorax of adult (from Grandi, 1950).

are preliminary to the pterygote line of evolution. It might be inferred, therefore, that the apterygote type of pleural sclerotization is primitive, the Collembola being the oldest known hexapods, and that from it has been derived the thoracic pleuron of the Pterygota.

Evidence of the derivation of the pterygote pleuron from two supracoxal sclerotic arches may be deduced from a comparative study of larval and adult Plecoptera. In the larva of *Perla* (fig. 9 E), for example, the membranous pleural area of the prothorax contains a typical anapleurite and a catapleurite. The catapleurite is articulated with the coxa, and from its anterior ventral angle a trochantinal bar (*Tn*) extends down to the lower angle of the coxa. The inner surface of the anapleurite (*F*) is crossed by a ridge (*PIR*) in line with the coxal process (*CxP*) of the catapleurite. The same pleural structure, as shown by Marta Grandi (1950), may be present on the other thoracic segments of the larva (*G*) and on the prothorax of the adult (*H*). In the winged segments of the adult, however, the pleuron has the typical pterygote structure (*H*, right), including basalar and subalar sclerites (*Ba*, *Sa*).

During development of the plecopteran from larva to adult, according to Grandi, the anapleurite of the larva unites with the posterior dorsal part of the catapleurite to form the adult episternum (fig. 9 H, *Eps*), and the ventral arm of the catapleurite becomes the trochantin (*Tn*). The epimeron (*Epm*), however, is mostly a secondary sclerotization not derived from the larval plates. The pleural sclerotization of larval Plecoptera, Grandi says, thus undergoes a gradual transition to that of the typical adult pleuron of the Pterygota.

The prothorax of a winged termite (fig. 9 D), as figured by Fuller (1924), also suggests the evolution of the pterothoracic pleuron from two supracoxal arches (*Apl*, *Cpl*), though Fuller did not so interpret it. Verhoeff (1902) analyzed the pleuron of the other pterygote insects into similar anapleural and catapleural components, which he homologized with supracoxal sclerites of *Lithobius forficatus*. It must be noted, however, that the pleural sclerotization is highly variable in different groups of chilopods, and, as has been shown, the principal plates appear to be derivatives of the coxae.

Convincing evidence of a primitive subcoxal limb segment would be the finding of an arthropod, modern or fossil, with a functional leg segment proximal to the coxa. It is true that a "subcoxa," or "precoxa," has often been described and figured in illustrations, but the segment becomes subcoxal by shifting the name "coxa" to the next segment or giving it to an imaginary segment. Since the coxa is

usually the functional basal segment of the limb on which most of the body muscles of the appendage are attached, if there was primarily a functional subcoxa, it should be explained how the muscles became transferred from the subcoxa to the coxa.

The writer himself formerly (1927) advocated and elaborated the subcoxal theory of the origin of the thoracic pleura, and devised a set of diagrams purporting to show the evolution of the insect pleuron from a subcoxal segment of the leg. Hansen (1930, pp. 75, 76) made some pungent remarks about the writer's subcoxal diagrams, and expressed it as his opinion that they "belong to fiction or poetry." The author of the diagrams makes no claim to being a poet, but does admit that he may sometimes have had uncontrolled flights of imagination.

A general survey of the pleural sclerotization in the several arthropod groups shows that there is no common pleural structure, and suggests that the various types of sclerotization in the lateral walls of the body segments are specific adaptations to the structural needs of each kind of animal. While the term *pleuron*, meaning the lateral sclerotization of a body segment, therefore, has no specific morphological significance, it is nevertheless by definition a convenient and useful name to retain for descriptive purposes.

The major segment plates of the arthropod skeleton—*tergum*, *pleura*, and *sternum*—are subject to subdivision into *tergites*, *pleurites*, and *sternites*. The subdivisions may be separated by membranous lines or areas in the integument. More often, however, they are demarked by grooves, commonly known as "sutures," which form internal sclerotic ridges to strengthen the skeleton or to give attachment to muscles. Clearly, neither membranous lines of the integument nor ridge-forming grooves are sutures in a literal sense of the term, which should imply lines along which originally distinct sclerites have secondarily united (*sutura*, a seam). A better term for such impressed lines is *sulcus* (a groove, or furrow), reserving the term *suture* for lines or grooves that can be demonstrated to be formed by the union of sclerites. The skeleton of arthropods, especially that of the insects, has been studied too much as a map, without giving attention to the mechanical significance of its structural features. On the other hand, arthropod morphology is becoming overloaded with theories.

V. INTERSEGMENTAL MECHANISMS

Since the arthropod body wall is continuous, it is not truly "divided" into segments. The functional body segments of the adult animal.

as already explained (p. 11), are merely the sclerotized parts of the primary segments separated by unsclerotized membranous areas. These so-called "intersegmental" membranes are the posterior parts of the primary segments, and each is generally folded into the preceding segment to allow movement of consecutive segments on each other. Particular types of structure, however, may limit the intersegmental movement to the horizontal or the vertical plane, and devices are sometimes present for separating the segments as far as the intersegmental membranes will allow.

Chilopoda.—The centipedes differ from most of the other arthropods in that they make lateral undulatory movements of the body as they run around objects obstructing their paths. This facility is owing in part to the fact that the tergal plates are limited to the back and do not curve downward on the sides. The intersegmental structure between the terga and sterna differs in the several chilopod groups.

A simple intertergal condition is seen in the agile lithobiids. The tergal plates overlap from before backward (fig. 10 A) and are connected by the infolded intersegmental membranes. When the terga are pulled apart and viewed from the inner surface (B), the membranes (*isMb*) are seen to be relatively narrow medially and expanded laterally where they merge into the pleural membranes (*plMb*). This arrangement allows the terga to be freely movable on each other in the transverse plane. The posteriorly overlapping sternal plates are connected by deeply inflected membranes, which also widen laterally. The body is traversed by longitudinal muscles that pull the segments together, and produce also the lateral movements, but there is no specific mechanism for pushing the segments apart. The intersegmental structure of *Scutigera* is essentially the same as in *Lithobius*. Manton (1952b) notes that "in the anamorphic Chilopoda, *Lithobius* and *Scutigera*, the length of the body in resting and running animals does not differ materially."

In a scolopendrid the tergal plates seen from above (fig. 10 C) overlap and seem to be the same as in *Lithobius*. A lengthwise section through the overlap (D), however, shows that it is the posterior part of the tergum itself (*Rd*) that is underfolded, and is attached to the anterior margin of the next tergum by only an extremely narrow connecting membrane (*isMb*). The reduplication, or infolded part of the tergum (E, *Rd*), is flexible, being somewhat thinner than the exposed part, and is marked by a fine transverse striation, which is weakly visible also on the rest of the plate. The narrow connective strip of membrane between the margins of the terga abruptly widens

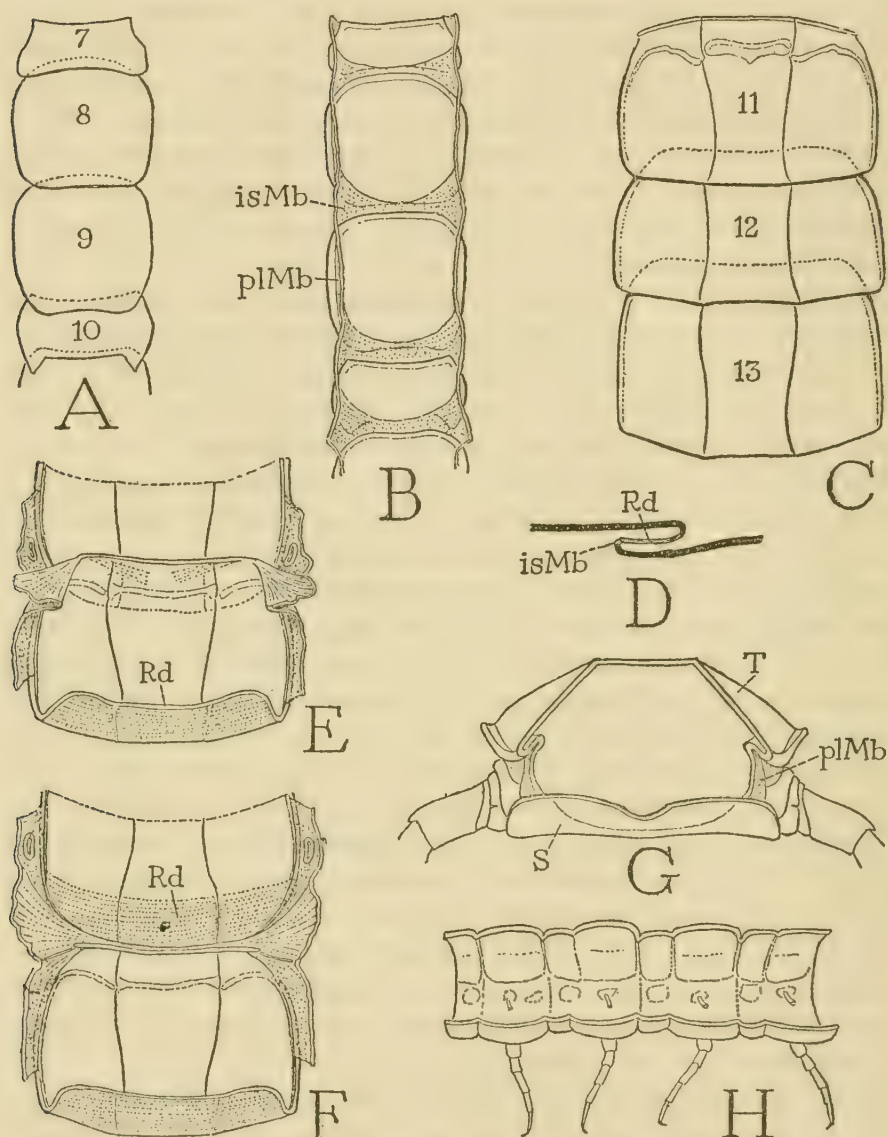


FIG. 10.—Intersegmental mechanisms, Chilopoda.

A, *Lithobius* sp., tergal plates in normal position, dorsal. B, Same, plates pulled apart, ventral, showing intersegmental membranes. C, *Scolopendra heros castanciceps*, tergal plates normally overlapping. D, Same, section of adjoining parts of two terga. E, Same, inner surfaces of adjoining terga in normal position. F, Same, plates forcibly pulled apart. G, Same, fourteenth segment, anterior. H, *Arenophilus bipuncticeps*, right half of segments, mesal.

on each side and is folded in a pocket where it joins the pleural membrane. When two consecutive terga are forcibly pulled apart (F) the lateral folds are flattened out and are seen in their full extent. It is evident that here sidewise movements of the segments on each other must depend largely on the flexibility of the posterior infolded parts of the terga. Within each fold are two small transverse muscles (E) arising medially on the anterior tergum and attached laterally on the margin of the posterior tergum. The pleural areas of *Scolopendra* (G) are mostly occupied by sclerites surrounding the bases of the coxae. The sternal plates (S) are separated by deep infolds of the integument, in which is a pair of small lateral sclerites that appear to belong to the segment following. *Scolopendra* has a strong and elaborate body musculature.

According to Manton (1952b) the body of a scolopendrid running at a fast gait may lengthen as much as 5 percent of its normal length. Since there is no protractor mechanism between the segments, the stretching of the body must result from a drag by the posterior legs exerted on the flexible tergal reduplications.

The geophilomorph chilopods present an intersegmental condition that is quite different again from that of either *Lithobius* or *Scolopendra*. A longitudinal section of the body of a species of *Arenophilus* (fig. 10 H) shows that there is no overlapping of the segmental plates, the segments being separated only by shallow indentations of the integument. The whole body is soft and flexible; a dead specimen can be stretched slightly by a flattening of the segmental plates. Manton (1952b) says that an individual running at a fast gait is only 3-6 percent longer than one going slowly. According to Dr. R. E. Crabill of the U. S. National Museum, *Arenophilus bipuncticeps* is adept at going either forward or backward. The movements of the legs and the accompanying undulations of the body by the chilopods are fully described and illustrated by Manton (1952b).

Insects.—Among the insects, particularly those that make respiratory movements of the abdomen, the abdominal segments in some species can be muscularly protracted as well as retracted. More commonly the respiratory movements consist of dorsoventral dilations and compressions of the segments, but both longitudinal and vertical movements may take place at the same time, as in the bees.

The typical longitudinal muscles of the insect abdomen (fig. 11 A, *rmcl*) retract the segments in the usual manner. The opposite movement of protraction is produced by short muscles (*pmcl*) lying in the intersegmental folds between successive terga and sterna. They take

their origins on the posterior parts of the segment plates and are inserted on apodemes (*Ap*) of the plate following that project forward into the preceding segment. Contraction of these muscles pushes the segments apart (*B*) as the connecting membranes become folded. Inasmuch as the retractors and protractors are both longitudinal muscles, which typically are of segmental length, it might be supposed that the protractors have shifted their origins to the rear parts of the

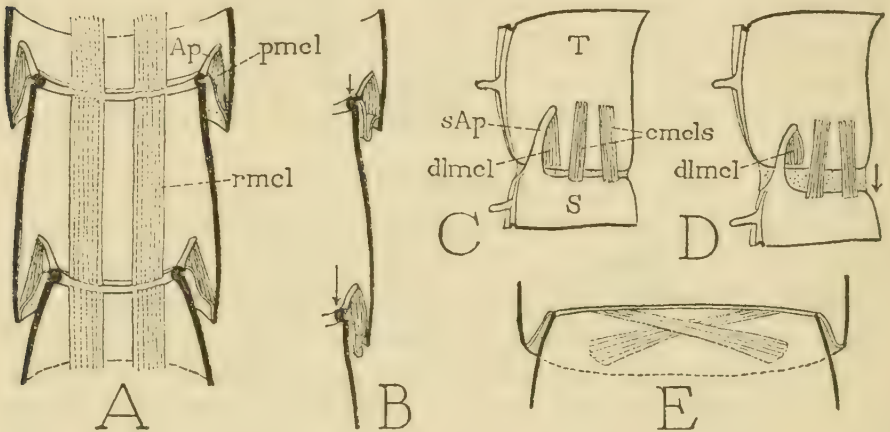


FIG. 11.—Abdominal mechanisms of insects, diagrammatic.

A, Consecutive terga in state of retraction, inner surface. B, Section of same protracted. C, Right half of segment, mesal, sternum elevated by compressor muscles (*cmcls*). D, Same, sternum depressed by dilator muscle (*dlmcl*). E, Oblique intertergal muscles of an acridid, giving movement of transverse torsion.

terga and sterna, while their insertions have been carried forward on the apodemes. However, this imaginary simultaneous migration of four muscles until their function becomes reversed is difficult to visualize; it would be more simple if we might assume that special muscles can be formed during evolution to operate a new mechanism.

A mechanism of partial torsion of the abdominal segments on each other is present at least in the Acrididae. Two intersegmental transverse muscles in the fold between two terga (fig. 11 E) cross each other from one side to the other, and evidently by antagonistic action give the adjoining segments a sidewise or rotary movement on each other.

The mechanism of dorsoventral dilation and compression works in the same way as that of protraction and retraction, but the operative muscles are antagonistic sets of vertical lateral muscles. The compressors are typical lateral tergosternal muscles (fig. 11 C, *cmcls*). Dila-

tion is produced by a reversed muscle on each side (*dlmcl*) arising on the lower edge of the tergum and inserted on the upper end of a long marginal apodeme of the sternum (*sAp*); by contraction it pushes the sternum downward (D).

Diplopoda.—The diplopods are so named because all their functional segments, except the first four or five bear each two pairs of legs. This fact is taken to mean that these four-legged segments are composed each of two wholly consolidated primitive segments. The doubling of the segments is explained by Manton (1954) as an adaptation to the habit of most diplopods of pushing into debris or under objects that obstruct their path, instead of running around such impediments as do the more flexible centipedes. "A marked ability to push," she says, "is as diagnostic of the Diplopoda as is the possession of diplo-segments." The union of the segments strengthens the body without the loss of legs, and is thus more effective for pushing or burrowing than would be twice the number of segments with the same number of legs. Manton tested the pushing ability of different species by harnessing them to flat-bottomed pans loaded with measured weights, assuming that the animals could push with a force equal to that with which they can pull. Members of the Polydesmoidea and Nematophora were found to be the strongest pushers among the diplopods.

The diplopods are noted for their ability to flex or coil the body ventrally by movement of the segments on each other. There is no protractor mechanism between the segments such as that found in the abdomen of some insects, and there are no intersegmental points of articulation. In the Proterandria the segments are solid rings connected by flexible membranes, and are shorter ventrally than dorsally. Ventral flexion and straightening are effected by the opposing action of antagonistic sets of body muscles.

The body segments of the Polydesmoidea are each distinctly differentiated into an anterior prozonite and a posterior metazonite (fig. 12 A, B). The longer metazonite is produced laterally into a pair of paranotal lobes (fig. 4 C). The prozonite is a simple ring with a smooth, polished surface, and is somewhat incurved anteriorly to fit into the preceding segment. In the extended position of the animal (fig. 12 A) the metazonite overlaps the prozonite of the following segment. The infolded connective membrane arises from the anterior margin of a posterior reduplication (*Rd*) of the tergum, which extends almost to the middle of the metazonite. Ventrally (B), however, the short sterna are entirely separated by wide, flat mem-

branes connecting the upcurved posterior margin of each sternum with the sternal prozonite of the next segment. In the flexed condition (B) the dorsal intertergal membranes are stretched out flat, and are just long enough to prevent a complete separation of the terga, so that the back of the animal makes an even curve. The sterna, on the other hand, come together, the prozonites overlapping internally the preceding sterna, and the connective membranes are deeply infolded.

The long cylindrical Julifornia have numerous short segments, which are only a little longer dorsally than ventrally. The anterior

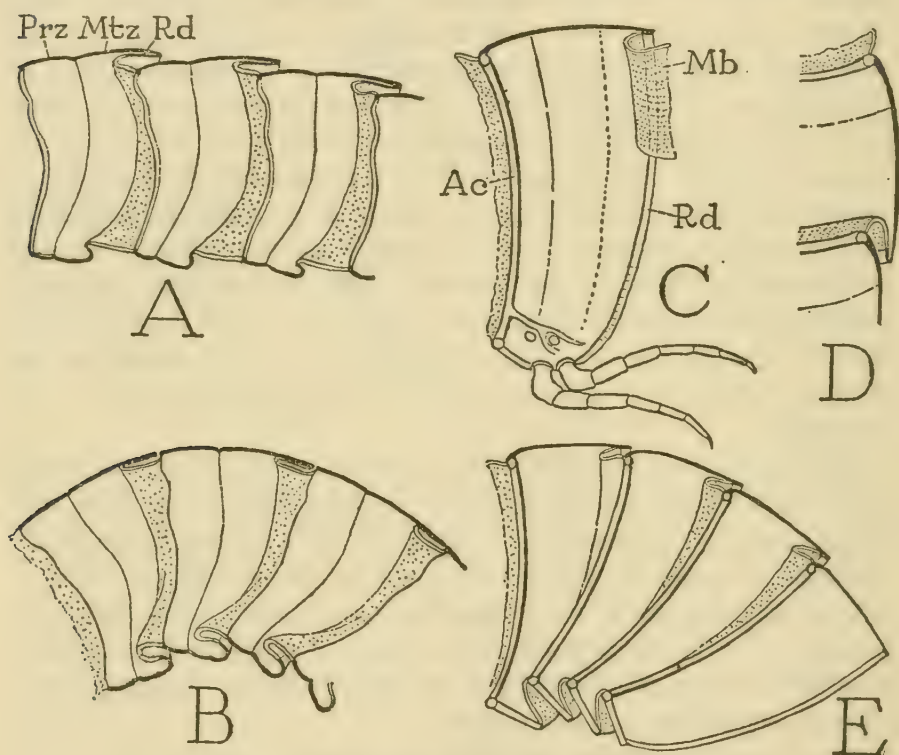


FIG. 12.—Intersegmental mechanisms, Diplopoda.

A, *Apheloria trimaculata*, Polydesmoidea, segments in straight position, mesal view of right side. B, Same, segments deflexed. C, *Narceus* sp., Juliformia, inner view of right side of a segment. D, Same, intertergal connection. E, Same, segments deflexed, diagrammatic.

margin of each segment (fig. 12 C) is thickened to form a strong internal ridge, the antecosta (*Ac*) or prothragma, for muscle attachments. The free posterior margin is a very narrow, rimlike reduplication (*Rd*) from the base of which arises the intersegmental membrane (*Mb*). In the straight condition (D) the metazonite widely overlaps the following prozonite.

Ventral flexion of the julid diplopod involves principally a compression and infolding of the ventral parts of the segments (fig. 12 E), which are pulled tight together. The terga are not separated enough to expose the intersegmental membranes, but the sterna are sharply tilted upward so that their anterior ends deeply overlap internally the depressed posterior ends of the preceding sterna. The segments are thus turned downward posteriorly. Though there is only a relatively small amount of movement between successive segments, the julids are able to curve themselves into a spiral because of the large number of short segments. The ball-and-socket nature of the intersegmental joints allows also a small degree of transverse rotation of the segments on each other. The body musculature and the function of the various sets of muscles concerned in the flexion of the diplopods has been fully described by Manton (1954).

Among the opisthandrious diplopods, members of the Oniscomorpha are noted for their ability to roll themselves up in a tight ball. A representative of this group will be described in the next section.

Crustacea.—The principal body movements of the malacostracan Crustacea are dorsoventral flexions of the abdomen on the thorax, and of the abdominal segments on each other. In the crayfish, for example, the successive segments of the abdomen are definitely hinged to each other by articular knobs on the posterior segmental margins at the bases of the lateral lobes of the terga (fig. 4 E, *x*, *x*). Movements of the segments on each other, therefore, are restricted to flexion and extension in a vertical plane. Dorsally each tergum widely overlaps the one behind it, and the two are connected by an ample infolded membrane. The narrow sternal plates by contrast, are separated by wide, flat conjunctivae that simply fold upward between the sterna when the abdomen is flexed. Owing to this intersegmental structure the animal is able to drive itself backward in the water by sudden, strong downward and forward strokes of the broad tail fan, as do also the shrimps and the lobsters. To accomplish this action the whole abdomen is filled with a great, complex mass of muscles, including bands of longitudinal fibers, segmental transverse muscles, and huge pleurisegmental oblique muscles, as shown by Schmidt (1915) in the crayfish *Astacus*, and by Berkeley (1928) in the shrimp *Pandalus*.

The ability of these crustaceans while peacefully swimming forward with the pleopods to suddenly dash backward on the appearance of danger is evidently of great importance to them for escaping from enemies in the water. The very musculature that enables them to

escape from aquatic enemies, however, has made them victims in greater numbers to a more ingenious terrestrial predator, on whose menus they have become favorite items.

The beach-living amphipods known as "sandfleas" are notorious jumpers. The abdomen (fig. 13 A, B) is differentiated into a larger anterior part of three ordinary segments (1, 2, 3) bearing typical pleopods, and into a smaller posterior part of three condensed segments (B, 4, 5, 6) and a small conical telson (*Tel*). The limbs of

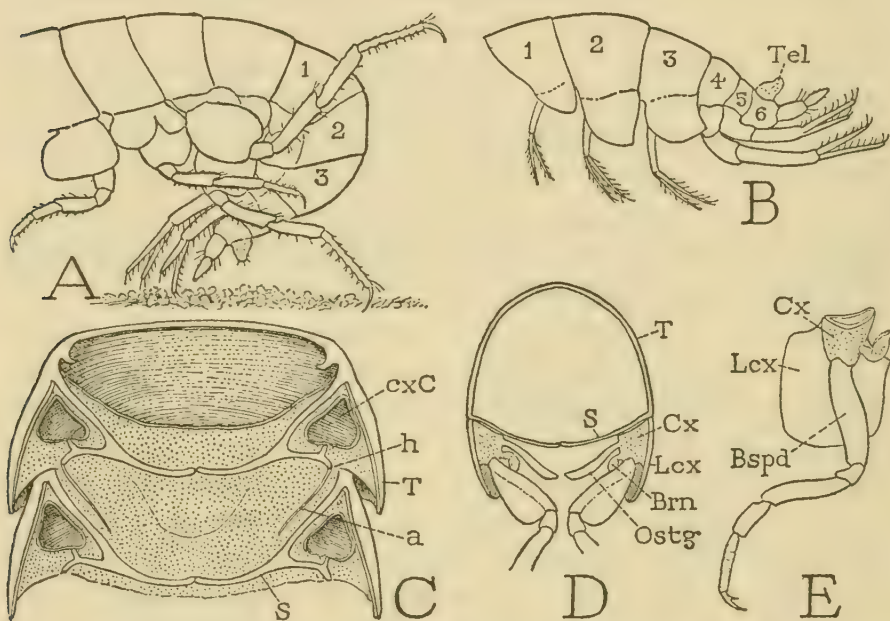


FIG. 13.—*Talorchestia longicornis*, Amphipoda.

A, Posterior thoracic segments and abdomen in flexed jumping position. B, Abdomen extended. C, Under surface of fifth and sixth thoracic segments, legs and coxal plates removed. D, Section of sixth thoracic segment of female, anterior. E, A right thoracic leg, mesal.

h, angle of flexion.

these posterior segments are thick, two-pronged appendages projecting backward and decreasing in length from the first to the third. The terminal part of the abdomen is the jumping organ of the sandflea. Its base is hinged dorsally to the large third tergum allowing the whole tail structure to be flexed downward and forward (A). With the prongs of the appendages braced against the beach sand, by a sudden straightening of the abdomen the amphipod makes a spring of remarkable distance, sometimes more than a meter.

The tergal plates of the thorax and the anterior three abdominal

segments are strongly arched and overlap each other from before backward. The under surface in *Talorchestia* (fig. 13 C) is weakly membranous except for a pair of narrow, delicate sternal bars (*S*) joined in the middle of each segment. The outer ends of the bars are widely forked into two arms that embrace the coxal cavities (*cx**C*). The longer anterior arm on each side goes forward and upward to join the margin of the tergum at the base of the lateral coxal plate (removed in the figure). The shorter posterior arm ends behind the coxa, and gives attachment to a slender bar (*a*) that turns mesally at a sharp angle and runs along the anterior sternal arm of the following segment. The consecutive segments are thus connected by V-shaped links, the apices of which (*h*) are the turning points of the segments on each other. Long bands of dorsal and ventral muscles run through the entire length of the thorax and abdomen, but the dorsal muscles are much larger than the ventrals. The weak, delicately membranous venter of the body allows a large degree of ventral flexion by the ventral muscles. The large dorsal muscles are the effectors of the backward stroke of the flexed posterior part of the abdomen by which the amphipod springs forward.

VI. FOLDING AND ROLLING ARTHROPODS

The device of flexing the body in a U-shaped fold or of rolling up in a ball to protect the soft under surface has been made use of by arthropods of several groups, as well as by such mammals as the hedgehog and some armadillos.

The first arthropods that practiced folding, bringing the venter of the posterior half of the body close against that of the anterior half, were the trilobites (fig. 14 A). The species of *Phacops* shown in the figure is a Devonian trilobite, but many of the earlier forms did the same thing. Among modern arthropods folding and rolling occur among the isopods, the diplopods, and the Acarina.

Most of the land isopods are adept in ventral flexion of the body. Some fold the body together in the manner of the trilobite; others such as *Armadillo* and *Armadillidium* roll themselves into a ball, and have thereby acquired the name of "pillbugs." A folding species is *Cylisticus convexus* (fig. 14 B), described by Gruner (1953) as a "Halbkugler." A detailed description of the skeleton and musculature of this isopod, with comparative studies on other species, is given by Gruner, from whose paper the following extract is taken.

The thoracic terga of *Cylisticus* are strongly calcified and widely overlap posteriorly. Transversely they are arched, more so than in

such forms as *Porcellio* (fig. 5 A), but less than are the terga of *Armadillidium* (fig. 14 D). The sterna by contrast are flatly convex, weak, and but little calcified. The ventral intersternal membranes are folded posteriorly so that each overlaps internally the following sternum. This feature, Gruner points out, is of much importance for ventral flexion and folding of the body. Where the terga and sterna come together the sternum has a notch on its posterior border that receives the margin of the following tergum. The segments are thus articulated on each other in a manner to allow of only an up-and-down movement.

Members of the genus *Armadillidium* (fig. 14 C) give a good ex-

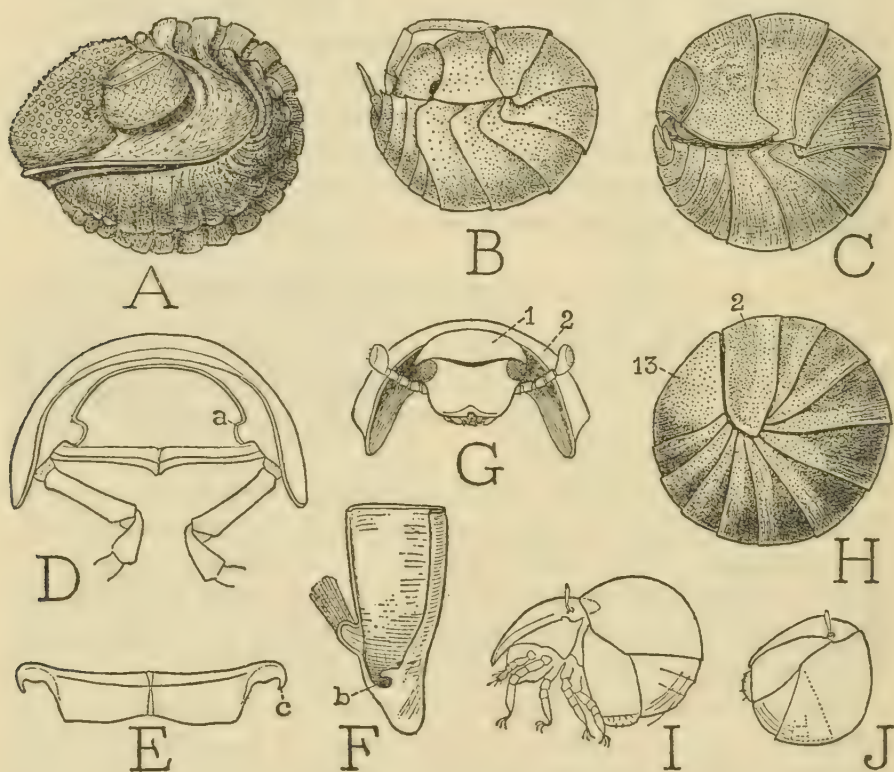


FIG. 14.—Folding and rolling arthropods.

A, *Phacops* sp., a folded Devonian trilobite. B, *Cyclisticus convexus*, a folded isopod (from Gruner, 1953). C, *Armadillidium vulgare*, a rolled isopod. D, Same, a thoracic segment, anterior. E, Same, a thoracic sternum. F, Same, lower end of a thoracic tergum, inner surface. G, *Sphaeropoeus* sp., head, collum (1), and second tergum (2). H, Same, completely rolled. I, *Acdelophora glomerata*, a water mite (from Grandjean, 1932). J, Same, rolled by compression (from Grandjean, 1932).

ample of isopods that roll themselves up in a spherical ball. In the rolled condition of *Armadillidium* the uropods cover the antennae and the mouth parts, but the top of the head is fully exposed. The thoracic terga are strongly arched transversely (D) and connected by deeply infolded membranes. The anterior tergal margin is produced into a small apodemal lobe on each side (D, *a*) on which is inserted a thick, transversely oblique muscle from the preceding tergum. The thoracic sterna (D, E) are thin, weakly sclerotized plates, each of which is divided into lateral halves by a hinge joint in the middle. The ends of the sternal plates are produced into lobes before the leg bases, each of which terminates in a recurved hook (E, *c*) inserted into a notch on the inner face of the lower part of the tergum (F, *b*).

The isopod body musculature includes dorsal and ventral longitudinal muscles, and dorsoventral muscles, and has been described by Gruner (1953) for *Cyclisticus* and *Armadillidium*. The dorsal muscles are mostly of segmental length and straighten the body after flexion, but in such forms as *Porcellio*, according to Gruner, some of the dorsal muscles extend through two segments, and these nonrolling species can bend the body upward. The ventral muscles of the isopods are two long lateral bands extending from the head to the telson. The dorsoventral muscles serve to lift the weak sterna, and thereby elevate the whole ventral body wall. When the ventral and the dorsoventral muscles contract at the same time, the under side of the body is both shortened and lifted, resulting in a ventral flexion of the body, or in the rolling of those species that curve into a ball.

Various other adaptive modifications of the skeleton are shown by Gruner to be correlated with rolling. In *Porcellio*, for example, the terga are of equal size and the lateral margins form an even ventral line. In *Armadillidium*, however, the third and fourth terga are not so deep as the others, leaving a notch in the lateral margins that facilitates rolling.

Ventral flexion of the body has been carried farthest in the oniscomorph diplopods, which roll up to such an extent that not only the mouth parts and antennae, but also the head and the collum are all completely concealed beneath the large, hoodlike last dorsal plate (fig. 14 H, 13). This plate is the tergum of the thirteenth body segment, counting the collum (G, 1) as the first. It covers the membranous terminal segment that carries the two pairs of gonopods and the anus-bearing telson, and in the rolled condition its free posterior part overlaps the head and collum. The enclosure of the head and collum, however, is due not so much to the degree of rolling as to the

fact that these parts hang down from beneath the front margin of the large second segmental tergum (G) instead of projecting forward.

The Oniscomorpha differ from the proterandrious diplopods and resemble the isopods in the flatness of the under surface of the body, which, including the laterotergites, is arched upward (fig. 7 A), a feature necessary for rolling. The unusual structure of the under surface of the oniscomorphs, in which the pleura are small, independent spiracle-bearing plates, has been described in connection with the general discussion of the pleural modifications (p. 20). The structure, body musculature, and rolling mechanism of *Glomeris* have been fully described by Gruner (1953), and Manton (1954) has exhaustively analyzed the rolling mechanisms of *Sphaerotherium* and *Glomeris*, as well as the flexing and locomotor mechanism of the other diplopods. In Manton's discussions the identification of the spiracular plates of the Oniscomorpha (fig. 7 B, *pl*) as "sterna" is confusing. As already pointed out, the articulation of these plates with the lateral basal angles of the coxae can scarcely leave any doubt that the plates are anything else than pleural, except by changing the definition of pleuron.

Finally, there are the oribatid mites of the family Protoplophoridae that compress themselves into a compact ball. The dorsal skeleton of one of these mites (fig. 14 I), as described by Grandjean (1932), is divided into five plates. The first is a shieldlike lobe, the *aspis*, covering the gnathosoma, the genital region, and the legs. The second and third are strongly convex, segmentlike dorsal plates connected by an infolded membrane. The other two are lateral plates depending from the edges of the first dorsal plate. In the "rolled" condition (J) the mite assumes a spherical form quite as complete as that of the isopod (C) or the diplopod (H), but its manner of doing so is different. Instead of rolling, accompanied by a separation of the dorsal parts of the back plates, the mite becomes a ball by collapsing. The *aspis* is brought down tight between the lateral plates (J), concealing the gnathosoma and the legs, and the second dorsal plate slides *forward* within the first dorsal plate. Thus, while the trilobite, the isopod, and the diplopod take the spherical form by folding or rolling the body upon itself, the mite accomplishes the same thing by compressing the body into a ball.

VII. TAGMOSIS

There is no known adult arthropod, living or fossil, in which all the primitive trunk segments are distinct annuli. The union of segments into functional groups is called *tagmosis*. Examples of tagmata

are the head, thorax, and abdomen of the Mandibulata, the prosoma and opisthosoma of the Chelicerata.

The head tagma of the mandibulate arthropods varies much in its segmental composition. The simplest embryonic head is a large cephalic lobe (fig. 15 A, B, C, F, *emH*) on which the eyes and first antennae are developed. Later there are added to this embryonic head and consolidated with it from one to six primary body segments to form the head of the adult. The embryonic cephalic lobe is regarded by most arthropod morphologists as being originally itself a segmented part of the trunk, but the alleged segments are differently identified by different writers, resulting in much confusion in the literature on "head segmentation."

A body segment, according to most students of arthropod embryogeny, is to be identified as such by the presence of a pair of coelomic sacs in the embryonic mesoderm. In the adult animal, however, a segment is an independently muscled and movable section of the trunk, unless secondarily combined with other segments. The question, therefore, is: was there ever any such segmentation in the embryonic cephalic lobe—did it ever consist of independently movable sections with a segmental musculature? If so, no evidence of tagmosis remains either in the head of the embryo, or in the structure and musculature of the corresponding part of the adult cranium of modern arthropods. Convincing evidence of former segmentation in this part of the head must await the finding of an embryo with a segmented cephalic lobe, or the discovery of a fossil arthropod with independent segments before the segment of the second antennae.

Only by definition does the presence of cavities in the mesoderm constitute body segmentation. For this reason some writers have regarded the cephalic lobe of the arthropod embryo as the equivalent of the annelid prostomium, since each structure contains the primitive brain. In either case, whether the primary arthropod head was prostomial or a segmental tagma, it was a purely sensory structure in which were developed the ocular and antennal centers that became the major parts of the modern brain. Later, the segment of the second antennae, or also the segments of the feeding appendages, were added to it to form the definitive head.

The adult head of modern arthropods occurs in its simplest form among the Crustacea, and is best seen in the anostracan branchiopods, where it is not covered by a carapace. The head of *Eubranchipus* (fig. 15 H), for example, is a distinct cephalic capsule (*Prtc*) bearing the eyes and both pairs of antennae. It is therefore a tagma com-

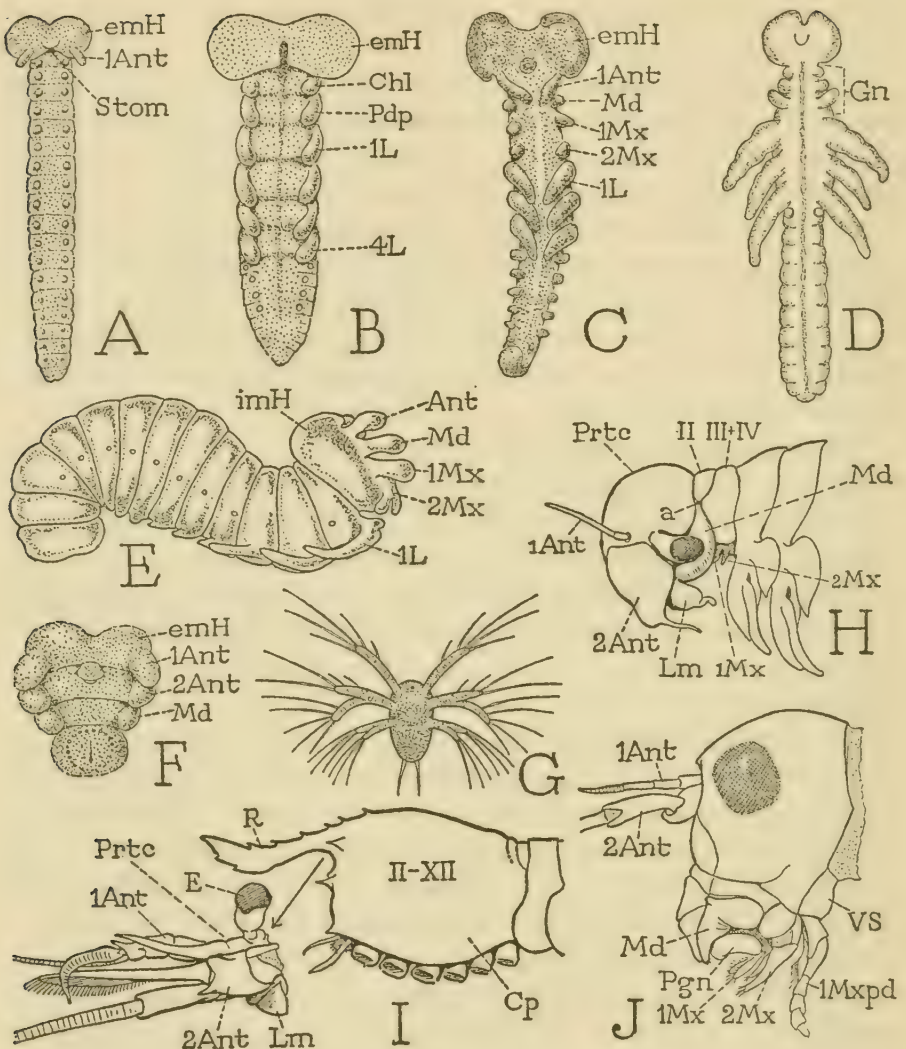


FIG. 15.—Tagmosis of the head.

A, Diagram of a fully segmented arthropod embryo. B, Embryo of a spider, *Agelena labyrinthica* (from Balfour, 1880). C, Embryo of a mantid, *Paratenodera sinensis* (from Hagan, 1917). D, Embryo of an hemipteron, *Ranatra fusca*, with differentiated thorax (from Hussey, 1926). E, An embryonic caterpillar, *Pieris rapae*, with imaginal head formed (from Eastham, 1930). F, Early stage of a crustacean embryo, *Leander serratus*, that develops in the egg (from Sollaud, 1923). G, A crustacean trochophore larva, *Penaeus sertiferus*, that hatches at a stage corresponding with F (from Pearson, 1939). H, Head and anterior body segments of an anostracan crustacean, *Eubranchipus vernalis*. I, Protocephalon of a decapod crustacean, *Spirontocaris polaris*, detached from beneath rostrum of carapace. J, Head of an amphipod crustacean, *Talorchestia longicornis*.

posed of the embryonic head lobe and the second antennal segment. Being the first step in the further evolution of the arthropod head, it may be termed a *protocephalon* (*Prtc*). In the anostracan the head is followed by a small independent mandibular segment (*II*) and the united segments (*III+IV*) of the greatly reduced first and second maxillae. In the other branchiopods all these segments are combined with the protocephalon in a composite head, which is covered by a head shield. In the primitive, newly discovered *Hutchinsoniella macracantha* (fig. 16 C, D) described by Sanders (1957), the shield covers only the head; in the Notostraca it is extended as a free fold over the anterior part of the body.

The protocephalon is again a discrete head unit in *Anaspides* and in most of the Malacostraca having a carapace (fig. 15 I); though normally hidden under the front of the carapace, it is easily detached as represented in the figure (*Prtc*). In these crustaceans the mandibular and maxillary segments are united with the thorax in a gnathothoracic tagma mostly covered by the carapace.

On the other hand, in the isopods and the amphipods the three gnathal segments and the first maxilliped segment have united with the protocephalon to form a composite adult head (fig. 15 J), which strikingly resembles the head of an insect, while the following thoracic segments remain free. Some entomologists, in fact, have regarded the isopods as possible ancestors of the insects, but the last segment of the insect head is that of the second maxillae, and in some of the isopods even the second maxilliped segment has been added to the head. The isopods and amphipods demonstrate, however, that within a single arthropod class, the embryonic gnathal segments may become either a part of the body or a part of the head. The union of the gnathal segments with the protocephalon seems to form the more efficient kind of head, since it combines the feeding organs with the major sensory organs of the animal, as in the vertebrate head, and has been adopted by all mandibulate arthropods other than crustaceans. In the diplopods and pauropods, however, the head appears to contain only two gnathal segments, the segment corresponding with that of the second maxillae being the first body segment.

The most uniform type of head among the mandibulate arthropods is that of the symphylans, the chilopods, and the insects, in which the mandibular segment and both maxillary segments are entirely incorporated in the adult cranium. In the early insect embryo, however, these segments are a part of the body behind the cephalic lobe (fig. 15 C), or they are condensed in a gnathal tagma (*D, Gn*) between the

embryonic head and the thorax. Finally, they completely unite with the embryonic head to form the imaginal head in the larva (E, *imH*) and the adult.

The insect embryo with well-developed legs (fig. 15 C), or with the thorax already differentiated from the abdomen (D), might suggest that in the evolution of the insects the thorax was developed as the locomotor center before the gnathal segments were added to the head. We cannot be sure, however, that the embryo follows the phylogenetic timetable. With insects that develop first into a larva, the differentiation of the thorax may be delayed to the pupal stage. A caterpillar (E) has short legs, but no differentiated thorax, and in legless larvae the legs are suppressed as external growths in the embryo. The structure of the embryo, therefore, does not necessarily reproduce the form or appearance of a primitive insect; it is only in its fundamental organization that the embryo can be taken to repeat evolutionary development. The large size of the head in the early arthropod embryo is due presumably to precocious growth expediting the development of the brain and optic lobes, just as the head of a vertebrate embryo is out of proportion to the size of the body, and does not mean that the early vertebrates were big-headed animals.

If the embryo leaves the egg at a very early stage of development, as with most of the Crustacea, it must be equipped at once for living an independent life. The course of its development in the egg, therefore, is directed to fitting the young animal on hatching for an active life. The crustacean nauplius larva (fig. 15 G) is equivalent to the early stage of an embryo that completes its development inside the egg (F), but the nauplius shows no division into head and body and no external segmentation; though it has first and second antennae and mandibles, these appendages have been modified to form swimming organs. In its later development the nauplius takes on the adult structure, either gradually or by assuming several successive metamorphic forms.

The Trilobita and the Chelicerata have no distinct head in the adult stage, because the head region is combined with the thorax in a cephalothoracic tagma, or prosoma; but still the arachnid embryo (fig. 15 B) may have a typical head lobe followed by distinct body segments, indicative that the embryonic cephalic lobe represents the primitive head of all the arthropods.

It is clear from these few examples of the structure of the head, that there is no standardized arthropod head with a uniform composition. The statement frequently made that the head of the mandibulate

arthropods is composed of six segments is contrary to the evidence from plainly visible facts, as shown by the writer (1951) in a comparative study of the head in the Mandibulata.

Tagmosis of the body segments is likewise variable. The centipede with its uniformly segmented body does very well in its special habitat, which it never leaves; but the centipedes have attained no such diversity of form as have the arachnids, the crustaceans, and the insects, in which the body structure is characterized by the association of segments to form distinct body regions with different functions. The diplopods might be said to have a multiple tagmosis in the union of the segments into double segments.

Since the arthropods are endowed with a superabundance of segmental appendages, it would appear that tagmosis primarily was an adaptation to limiting the walking appendages to a consolidated section of the body, commonly termed the thorax, leaving the post-thoracic section, or abdomen, freely movable. The thoracic limbs, however, may be secondarily modified for swimming if the animal has given up walking for swimming. The abdominal appendages in all cases except that of the myriapods have lost their leg structure, and are generally modified for special purposes, such as swimming, copulation, egg laying, respiration, and silk spinning. By this division of labor among the appendages the animal retains its locomotor power, and at the same time acquires tools for a variety of other uses. The three segments of the insect thorax became differentiated as a tagma when the legs of these segments took over the locomotor function, and those of the following segments were suppressed. With the thorax established as the locomotor center of the body, it later served as the basis for the development of wings.

Tagmosis is carried farthest in the Chelicerata, in which the primitive head (fig. 15 B) and the following six or seven segments are combined in a single body unit, the prosoma, carrying the eyes, the feeding appendages, and the legs, while the posterior segments constitute an opisthosoma, or abdomen. In *Limulus* and the scorpion the abdomen remains fully segmented, and *Limulus* retains the abdominal appendages in a modified form. In most of the spiders, however, external segmentation of the abdomen has been entirely suppressed, but the two parts of the body are separated by a narrow constriction, which gives freedom of movement to the abdomen. This is necessary to the spinning spiders, but seems an inconvenience to the ground-living species.

Finally, the ticks and most of the mites have attained the ultimate

in tagmosis by a union of all the body segments in a one-piece body. Only a small head structure, the capitulum, or gnathosoma, carrying the feeding organs remains free, but since no other arachnid has a similar headpiece, the capitulum is evidently a special development of the Acarina to facilitate their feeding habits.

The prevalence of tagmosis among the arthropods would indicate that, while body segmentation is the fundamental feature of arthropod organization, inherited from remote wormlike ancestors, modern arthropods have made their chief structural advances by partially suppressing it.

VIII. THE SEGMENTAL APPENDAGES

The arthropods stand apart from other animals by reason of the number of segmental appendages they possess, and it is very probable that primarily all their limbs were jointed legs, as are those of the trilobites (fig. 16 A), and served for walking. In the evolution of the arthropods, however, it was soon found that fewer appendages could serve as well for locomotion, and that the others could advantageously be converted into organs for grasping, feeding, swimming, copulation, egg laying, and numerous other purposes. Thus, to their polypod ancestors the modern arthropods owe their equipment with a great variety of anatomical tools, and the fact that they have thereby become the most diversified animals on the earth today. The quadripeds, the bipeds, and the apodous creatures had no such evolutionary possibilities.

The arthropod appendages, regardless of their adult form, all have the same origin in the embryo, namely, from paired, lateroventral, budlike lobes of the body segments (figs. 15 A, 17 A). Though "recapitulation" does not hold so prominent a place in zoological thought as it once did, it can hardly be renounced completely. The embryonic development of the arthropod appendages would seem to be a case in which recapitulation can be safely invoked in support of the idea that the embryonic origin and growth of the appendages repeats their phylogenetic history. As illustrated by Roonwal (1937) in *Locusta* (fig. 17 A-F) the legs develop from primary budlike rudiments by lengthening and becoming segmented until they attain the adult structure.

The legs of the Onychophora likewise begin in the embryo as simple buds (fig. 17 G), but since the onychophoran ancestors did not acquire a sclerotization of the cuticle, their legs of necessity remained short, thick, and unsegmented. However, the lateroventral position of the

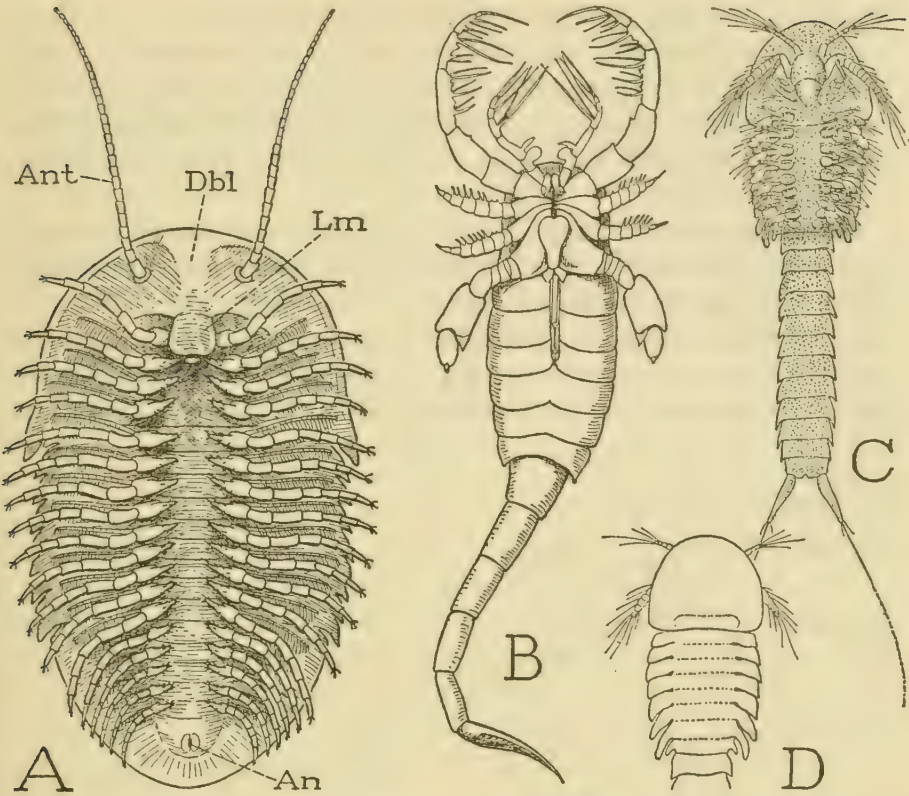


FIG. 16.—Examples of specialized palaeozoic arthropods, and a primitive modern crustacean.

A, Diagram of a trilobite, ventral surface and legs. B, A scorpionlike eurypterid, *Mixopterus kiaeri* (outline from Störmer, 1934). C, *Hutchinsoniella macracantha*, a primitive modern crustacean. D, Same, head and thorax, dorsal.

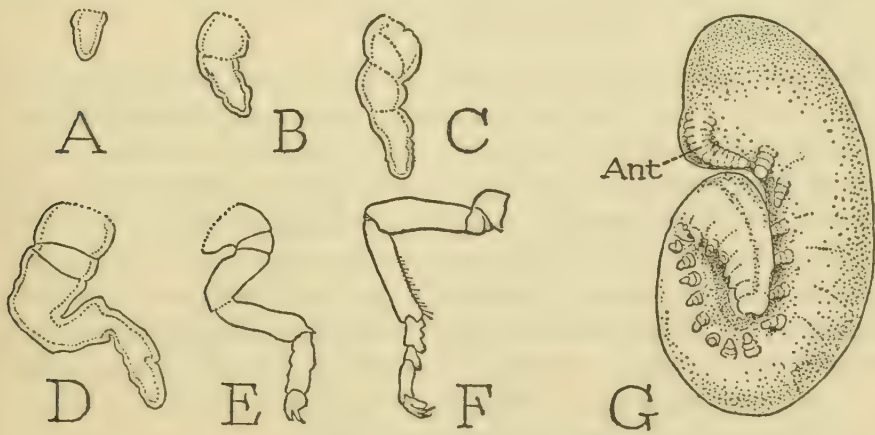


FIG. 17.—Embryonic development of legs.

A-F, Developmental stages of middle leg of a locust, from 70-hour embryo to newly hatched nymph (from Roonwal, 1937). G, Embryo of an onychophoran, *Peripatopsis moscleyi*, with appendage rudiments (outline from Manton, 1949).

onychophoran and arthropod limbs, their embryonic origin from simple lobes, and their musculature are all features that have no counterparts in the parapodia of the Polychaeta, and this fact discredits the often-expressed opinion that the limbs of the onychophorans and arthropods have been evolved from the parapodia of ancestral polychaetes.

Inasmuch as an arthropod limb is a tubular outgrowth of the body wall, its movable sections, or *podomeres*, are merely sclerotized parts of the tube, and the *joints* are short unsclerotized parts between them. The embryonic limbs are penetrated by mesoderm, which forms the intrinsic limb musculature, the fibers of which become attached on specific podomeres, but not necessarily on all of them. The muscu-

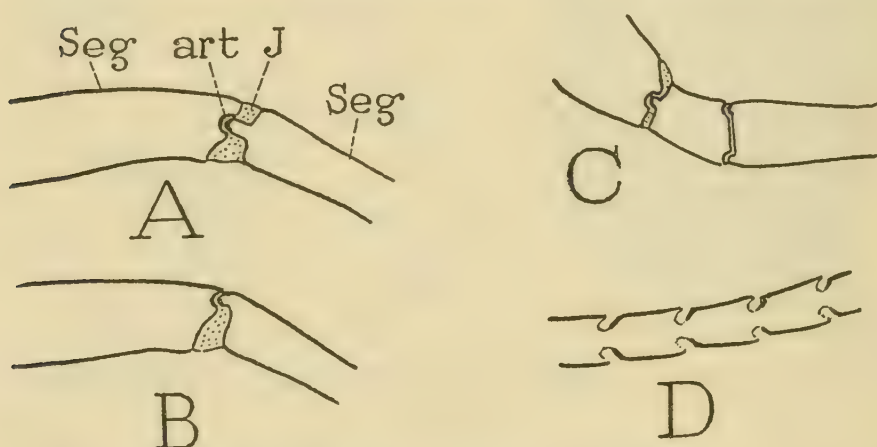


FIG. 18.—Limb segments, joints, and articulations.

A, Adjoining parts of two leg segments with articulated joint. B, Joint with single dorsal articulations. C, Double articulations, horizontal and vertical. D, Unarticulated joints of an antennal flagellum.

lated podomeres constitute the true *segments*, or *podites*, of the limbs (fig. 18 A, *Seg*). A segment, however, may be subdivided into non-musculated subsegments, and in the joints there are sometimes present small rings without muscle attachments. These minor parts of the limbs have been counted as "segments" by some writers, who thus confuse the true segmentation and the segment nomenclature. Subdivisions of the tarsus, for example, are tarsomeres, but are commonly called "tarsal segments" by taxonomists. The only known case of tarsomeres being individually musculated is in the ovigerous legs of a male pycnogonid. Finally, the term "joint" should not be used for a leg segment, though it often is so used.

In order to limit the movement at intersegmental limb joints, the

ends of the adjoining segments are specifically articulated on each other. An *articulation* is usually formed by the extension of an articular process from the base of the distal segment through the joint membrane received in a socket on the end of the proximal segment (fig. 18 A, *art*). There may be only one articulation at a joint (B), or two articulations. The hinge of a double articulation is sometimes horizontal, sometimes vertical (C). Since different types of articulations are usually present at different joints of the same leg, the leg as a whole is capable of varied movement. Articulations are generally absent at joints between nonmusculated subsegments (D), allowing free movement in any direction.

Failure to recognize that a muscled limb segment may be divided into nonmusculated subsegments has led to confusion in comparative studies on the arthropod antennae. It was shown by Imms (1939) that the antennae of most arthropods, including Collembola and Diplura among the hexapods, are composed of muscled segments, while those of thysanuran and pterygote insects have muscles only in the basal segment. On this apparent difference in the antennae, the tracheate mandibulate arthropods have been classed by Remington (1955) into Myocerata and Amyocerata. The actual difference between the two types of antennae, however, is not in the musculature, but in the number of segments. The basal stalk, or scape, of the insect antenna contains muscles inserted on the pedicel, and is a true segment. The pedicel may be a basal part of the flagellum, but more probably it is a segment from which muscles to the flagellum have been removed to make space for the organ of Johnston. The flagellum, having no intrinsic muscles, is a *single segment* usually subdivided into short rings, as are the flagella of crustacean limbs. The insect antenna, therefore, contains at most only *three* segments. The antennae of coleopterous and lepidopterous larvae (see Dethier, 1941) are usually composed of three simple segments, and even in adult brachycerous Diptera the antennae are clearly three-segmented, with the apical segment subdivided or not. It has furthermore been shown by Imms (1940) that true antennal segments are generated by subdivision of the apical segment, but that the flagellum grows from its base, as described also by Lhoste (1942) in *Forficula*.

The evolution of the limbs into jointed legs must have taken place in Precambrian times, since the limbs of the trilobites and their relatives were already fully segmented legs in the early Cambrian. If all the podomeres of a trilobite leg were true muscled segments, discounting the segmental nature of a small basal ring that Störmer

(1939) regarded as a "precoxa," the trilobites had eight-segmented legs (fig. 19 A). In the later evolution of the arthropods some of the original segments were lost, united, or subdivided, leading to confusion in attempts to name the segments consistently. However, we have long-established names for eight segments that can be consistently applied if we assume that the basal segment is the same in all groups and that segmentation in the telopodite is variable.

The basal limb segment, *coxa*, or *coxopodite*, gives attachment to the body muscles that move the limb as a whole, and therefore should be homologous in all the arthropods. Yet, when the limb contains eight segments, some writers have regarded the functional basal segment as a "precoxa," or "subcoxa," without explaining how the muscles become transferred to the coxa in a seven-segmented limb. In a few cases the coxa is immovably attached to the body, and the second segment then becomes the functional base of the limb, but it does not take over the coxal muscles.

The eight apparent segments of the trilobite leg (fig. 19 A) are subequal in length, except for the very small, three-clawed apical pretarsus. In the eurypterids (B) the last two legs appear to be nine-segmented, but two short rings following the coxa may be subdivisions of a segment since there is only one segment here in the other legs. In the legs of a modern pycnogonid (C) eight segments are typically differentiated. Following the coxa are two short trochanteral segments (*1Tr*, *2Tr*), a long femur (*Fm*), a patella (*Pat*), a slender tibia (*Tb*), a subdivided tarsus (*Tar*) of two tarsomeres, and a three-clawed pretarsus. These same eight segments are present in some of the legs of solpugid arachnids (D) and in the Acarina, though in the latter the second trochanter is much reduced in size. The scorpion (E) and most of the other arachnids have only seven leg segments by elimination of one trochanter, but the tarsus is divided into two subsegments. The patella is characteristically present in all the Chelicerata, including the Xiphosurida, which also have but one trochanter. In the trilobite leg (A) the fifth segment (*Pat*), therefore, is to be identified with the patella of the chelicerates.

The legs of the mandibulate arthropods (fig. 19 F-J) consistently lack a patellar segment. The malacostracan Crustacea (F) and the myriapods (G, H, I) have seven-segmented legs, there being two segments in the trochanteral region. The segments, however, differ much in relative size, showing that the size of a segment is no criterion of its identity. The apical segment is a simple, clawlike dactylopodite, or pretarsus. Finally the typical insect leg (J) is

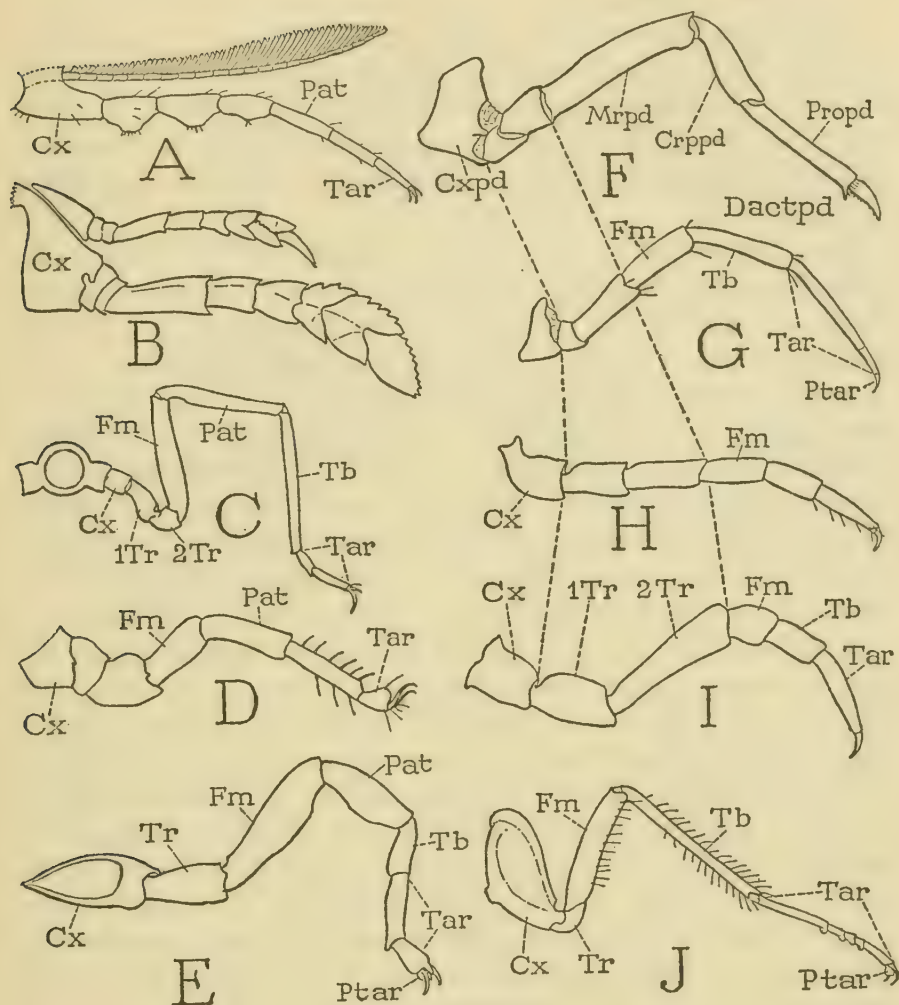


FIG. 19.—Comparative leg segmentation.

A, Leg of a trilobite, apparently 8-segmented, with coxal epipodite (from Störmer, 1939). B, Fifth and sixth legs of a eurypterid, apparently 9-segmented (from Clarke and Ruedemann, 1912). C, 8-segmented leg of a pycnogonid. D, 8-segmented leg of a solpugid arachnid. E, 7-segmented leg of a scorpion. F, 7-segmented leg of a crustacean, *Cambarus*. G, 7-segmented leg of a chilopod, *Lithobius*. H, Leg of a julid diplopod, 7 subequal segments. I, Leg of a polydesmoid diplopod, 7 segments of unequal length. J, Typical 6-segmented insect leg, *Periplaneta*.

six-segmented, having only one trochanter, a subdivided tarsus, and a two-clawed pretarsus.

It is evident that the different leg segmentation among the arthropods has come about principally by the elimination of segments, either of one of the trochanters or of the patella, or both. Rarely it is apparent that adjoining segments have united, but there is no clear case of a segment having been divided into two true muscled segments.

The end segment, dactylopodite, or pretarsus, of the walking legs undergoes numerous modifications to give it a more efficient grasping or clinging function. In the crustaceans and myriapods this segment is a simple claw. In the pycnogonids, arachnids, and insects a pair of accessory lateral claws arises from the base of the dactylopodite, forming thus a three-clawed foot, or a two-clawed foot if the median dactyl is suppressed. The typical pretarsus of adult insects is two-clawed, but in some of the apterygote insects the median dactyl is retained. Generally the body of the insect pretarsus is produced as an adhesive lobe or pad, the *arolium*, projecting between or below the claws, which enables the insect to walk on vertical surfaces.

A similar adhesive pad is present on the feet of ticks and on the feet of the pselaphognathous diplopod *Polyxenus* (the latter described by Manton, 1956). Though it cannot be supposed that the adhesive pads in these forms are homologous with the insect arolium, their presence gives an interesting example of the independent development of similar structures for the same purpose. *Polyxenus* is exceptional among the diplopods in being able to walk on smooth vertical surfaces and even on the under sides of horizontal objects.

In the Chelicerata and Crustacea the pretarsus (dactylopodite) has both a levator and a depressor muscle. In the hexapods and the myriapods there is only a depressor muscle. Both muscles of the pretarsus in *Limulus*, Pycnogonida, and Crustacea arise in the tarsus (propodite), but in the other arthropods there is a tendency for one or both muscles to be extended into the more proximal segments of the legs. The persistent absence of the dorsal muscle in the myriapods and insects is difficult to explain functionally, but it should be a phylogenetic link between these two mandibulate groups.

The basal segment of a leg, the *coxa*, or *coxopodite*, is usually articulated on the body in such a manner that the whole appendage turns forward and backward on a transverse or transversely oblique axis. The primitive leg probably had dorsal promotor and remotor muscles arising on the segmental tergum and corresponding ventral muscles arising on the sternum (fig. 20 A). The sternal muscles

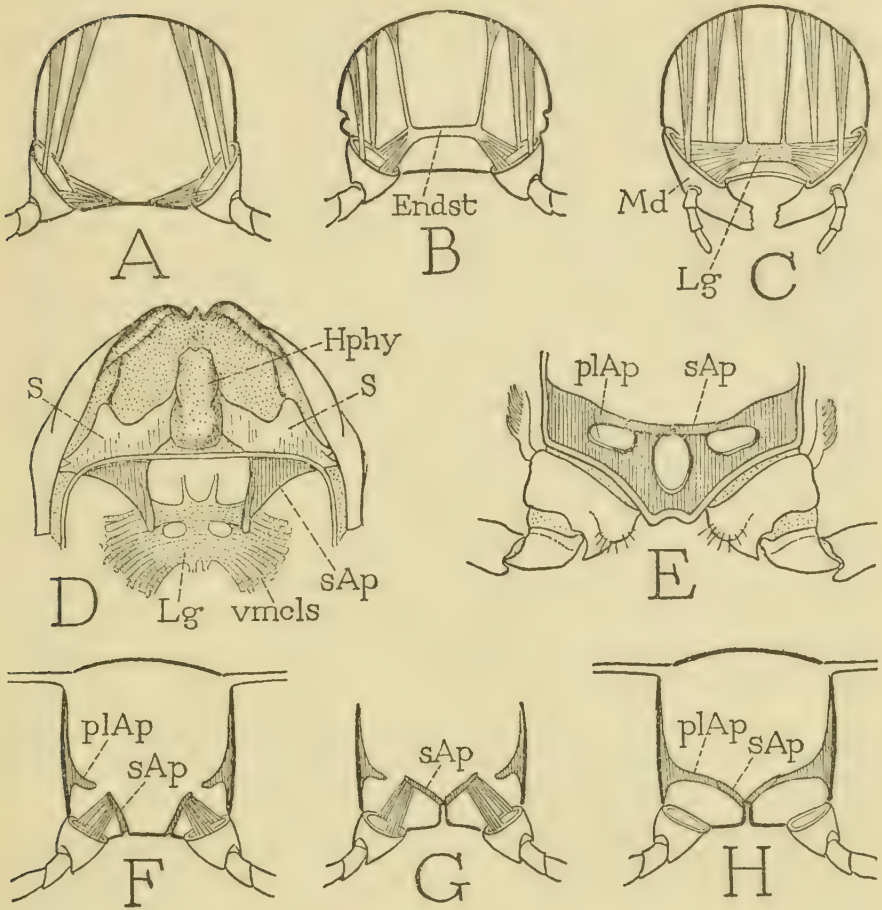


FIG. 20.—Illustrating various attachments of ventral limb muscles, mostly diagrammatic.

A, Probable primitive limb musculature. B, Ventral leg muscles of Chelicerata arising on a noncuticular "endosternum." C, Mandibles of a lower crustacean with ventral muscles arising from an intergnathal ligament. D, Ventral muscles of mouth parts of a chilopod arising from an intergnathal ligament supported on apodemes from premandibular sternal sclerites of head. E, Cross section of lower part of thorax of a decapod crustacean, *Cambarus*, showing united intersegmental pleural and sternal apodemes. F, Thoracic segment of a lower insect, ventral muscles of legs attached on intrasegmental sternal apodemes. G, Thoracic sternal apodemes of a higher insect elevated on a median sternal inflection. H, Union of pleural and sternal apodemes in thorax of an insect.

being practically horizontal were at a mechanical disadvantage, and in most modern arthropods their mesal attachments have been elevated. In most of the Chelicerata the ventral muscles of all the appendages arise from a platform, the so-called endosternum (fig. 20 B, *Endst*), suspended in the body by branches attached on the back. A similar structure is present in the gnathal region of some lower Crustacea, but usually it is contracted to the form of a thick transverse ligament uniting the inner ends of the opposing muscles of the mandibles (*C*, *Lg*). An intergnathal ligament of the same kind is present in the Diplopoda. Among the chilopods a broad, flat ligamentous plate in the head of Scutigermorpha (*D*, *Lg*) gives off the ventral muscles of the mouth parts, but it is supported on a pair of anterior ventral cuticular apodemes (*sAp*). In the other chilopods and in the symphylans the muscles have been taken over by the apodemes and the ligament disappears. In the insects the anterior, originally ventral, apodemes have united with a bar through the back of the head forming the endoskeletal structure known as the tentorium, on which the ventral muscles of the mouth parts are attached.

In the macruran Crustacea the ventral muscles of the thoracic appendages arise on an elaborate endoskeletal structure (fig. 20 E) composed of a series of united pleural and sternal apodemes (*plAp*, *sAp*) inflected from the intersegmental grooves between successive segments. All the muscles of the thoracic appendages in the crayfish arise on this structure and on the pleural plates; only the mandibles and the first maxillae have dorsal muscles from the carapace.

In some of the lower pterygote insects most of the ventral muscles of the legs take their origin on a pair of lateral sternal apodemes (fig. 20 F, *sAp*). In the higher orders, however, the two apodemes are approximated and are carried inward on a median inflection of the sternum (*G*), forming a Y-shaped structure known as the *furca*. The arms of the *furca* are often connected by muscles with pleural apodemes, but the pleural and sternal apodemes of each side are sometimes united (*H*), forming thus a weak imitation of the pleurosternal endoskeleton of the decapod (*E*). It must be noted, however, that the insect differs from the crustacean in that both the pleural and the sternal apodemes are *intrasegmental* and not intersegmental. A similar structure for the same mechanical purpose has thus been formed in different ways in the two groups.

Though the ventral muscles of the appendages are primarily producers and reducers, when the sternal articulation of the limb is eliminated these muscles become adductors. This change of function

occurs particularly with the ventral muscles of the gnathal appendages, in which adduction is the important movement.

The segmental appendages of the arthropods were developed in the first place for locomotion, and, though a variable number of them have been modified for other purposes, in each major arthropod group some of the limbs have retained the primitive leg structure and are still used for walking, except where all the legs have been converted into swimming organs. In a series of papers on "The Evolution of Arthropodan Locomotory Mechanisms," Manton (1950, 1952a, 1952b, 1953, 1954, 1956) has described the skeleto-muscular mechanism of locomotion and the leg movements of an onychophoran and representatives of the various groups of walking arthropods. "The locomotory mechanism shown by *Peripatus*," she says, "provides a key to the understanding of the evolution of the various mechanisms found in the higher Arthropoda." This fact, perhaps, may be taken to mean that locomotion by walking was first developed by common ancestors of the two groups.

The differentiation of the primitive arthropod legs into organs for purposes other than walking or running has been due in large part to the development of outgrowths of various kinds from the outer and inner surfaces of the limb segments. Such structures are known as *exites* and *endites* respectively.

Exites in the form of long, pectinate branches that perhaps served as gills were present on the basal leg segments of such Cambrian arthropods as *Marella*, *Burgessia*, and the trilobites (fig. 21 B, *Eppd*). In modern Crustacea branchial exites are commonly borne on the leg bases. A coxal exite is designated an *epipodite* regardless of its function.

Many of the Crustacea, particularly larval forms, have a variously developed exite on the second limb segment, or basipodite, which is known as an *exopodite* (fig. 21 A, *Expd*) because it gives the appendage the appearance of being two-branched. The trilobite epipodite has often been mistaken for an exopodite, but these two limb branches, being on different segments, are clearly not homologous. The trilobite leg, therefore, is not "biramous" in the manner of a crustacean limb, and does not relate the trilobites to the Crustacea. It is not clear what the primary function of the exopodites may have been, but in many crustacean larvae these branches on the cephalic and thoracic appendages bear brushes of long setae that facilitate the temporary use of these limbs as swimming organs. The exopodites may then be reduced or lost when the pleopods of the adult assume

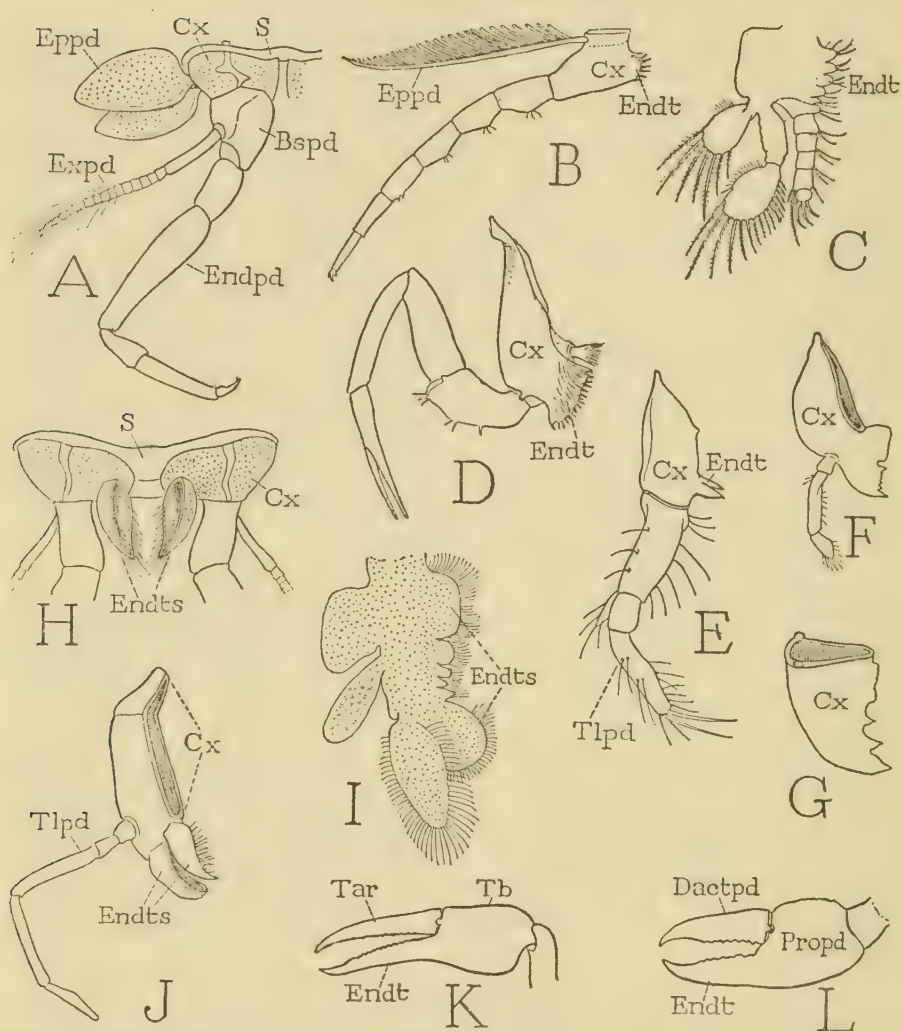


FIG. 21.—Development of exites and endites on arthropod limbs.

A, A biramous crustacean limb, left pereopod of *Anaspides*, posterior. B, A uniramous trilobite leg with coxal exite and endite (from Störmer, 1939). C, Thoracic limb of the primitive crustacean *Hutchinsoniella*. D, Fourth leg of *Limulus*. E, Leglike mandible of an ostracod, *Philomedes*. F, A crustacean mandible with reduced telopodite. G, An insect mandible, telopodite eliminated. H, Bases of sixth or seventh thoracic limbs of *Anaspides* with coxal endites. I, A phyllopodial branchiopod limb with segmental endites, segmentation suppressed. J, An insect maxilla. K, Pedipalp chela of a scorpion. L, Chela of a decapod crustacean.

the swimming function. The pleopods, on the other hand, usually retain the biramous form, but they never have the structure or segmentation of functional legs, suggesting that their growth is arrested at an early stage of development—if they ever were functional legs.

The development of endites, particularly on the coxal segments of the limbs, has been of great importance in the later evolution of all the arthropods. The coxae of the trilobite legs are produced mesally into spiny lobes directed somewhat forward (fig. 16 A), which evidently served for securing food and passing it along to the mouth by the action of the legs. The legs of *Limulus* are equipped with similar spiniferous coxal processes (fig. 21 D), but none of the Chelicerata has developed true masticatory jaws. Coxal endites play only a subsidiary feeding role in the arachnids by enclosing a preoral food cavity.

A particularly important result of the development of coxal endites was the evolution of a specific pair of appendages as jaws, or *mandibles*, that became distinctive of the mandibulate branch of the arthropods. The mandibles are simply the coxae of a pair of primitive legs associated with the mouth having strongly developed gnathal endites opposed to each other. The distal part of the limb is retained in some Crustacea (fig. 21 E, F) as a palpus, but in the other mandibulates it has been discarded as useless (G). The gnathal endite of the mandible is usually a solid outgrowth of the coxa, but in the diplopods and symphylans it has become an independently movable lobe, which is itself the functional jaw. Though the mandibles are generally biting and chewing organs, they may be prolonged into a pair of grasping fangs, or drawn out into slender piercing stylets.

To be effective as jaws the mandibles have lost the primitive leg articulation on the sternum so that they swing transversely on the lateral hinges; the ventral muscles then become adductors. A mandible of the primitive type has thus only a single lateral articulation on the head or the mandibular segment, but in some of the higher crustaceans and in most of the biting insects they have acquired a secondary anterior articulation on the epistome or the clypeus, so that they swing more effectively on fixed horizontal axes close to their outer margins. In most of the insects the primitive adductor ventral muscles have been eliminated, and the operation of the mandibles is taken over entirely by the dorsal muscles.

The maxillae also owe much of their function as food manipulators to the presence of coxal endites, which, however, are highly diverse in form, as are the maxillae themselves. The insect maxilla (fig. 21 J)

usually retains the telopodite as a segmented palpus, and bears two endite lobes on the end of the coxa. The most leglike maxillae are those of the second pair in the chilopod *Scutigera*, which are simple, segmented appendages with a slender endite on the coxa. Crustacean maxillae retain so little of the leg structure and are so various in form that it is often difficult to identify their parts.

Endites are not commonly present on the legs of mandibulate arthropods, except in the branchiopods. The flattened, unsegmented thoracic limbs of these crustaceans may have as many as six lobes on the inner margin, together with an apical lobe (fig. 21 I), suggesting the usual seven segments of a walking leg. The development of these appendages shows, in fact, that they begin as slender leglike limbs, and later take on the flattened, lobulated phyllopodial form. In the amphipods and isopods coxal endites are highly developed on the thoracic legs of the female to form a brood chamber in which the eggs and the young are carried (fig. 5 B, *Ostg*). In the crustacean *Anaspides* membranous, scoop-shaped, setigerous endite lobes with concave surfaces toward each other (fig. 21 H, *Endts*) are borne on the mesal surfaces of the coxae of the sixth and seventh thoracic appendages of the female. When the body is flexed ventrally the endites come together and apparently form a passageway for the eggs from the openings of the oviducts to the spermatheca on the venter of the eighth segment.

The egg-laying apparatus, or ovipositor, of female insects has usually been regarded as formed of coxal endites on the appendages of the eighth and ninth abdominal segments, but recently Matsuda (1958) has contended that the ovipositor blades (valvulae) are secondary outgrowths of the sterna, as claimed formerly by Heymons (1899). Likewise the complex external genital structures of male insects have commonly been interpreted as modified segmental appendages, but evidence against their leg origin has been presented by the writer (1957) and independently by Matsuda (1958).

On the distal parts of the limbs the development of endites has enabled various arthropods to be equipped with grasping organs, or chelae. In the Crustacea (fig. 21 L) a chela is formed by an endite process of the propodite opposed to the movable dactylopodite. In the scorpion (K), on the other hand, the movable member of the chela is the tarsus, or the fused tarsus and pretarsus, and the fixed claw is an endite of the tibia. The same is true of the leg pincers of *Limulus*, except those of the last legs. Various other implements have been fashioned on the legs, such as the pollen brushes, the

antenna cleaners, and the pollen-collecting apparatus of the bees.

If we had lived in the time of the lobopod ancestors of the arthropods, we should never have suspected the potentiality that lay in their simple feet, which has led to the future development and diversification of the modern arthropod appendages. But who, also, would have supposed that the fins of the coelacanth fishes 300 million years ago would ever develop into the legs of mammals or the human arm and hand? It is only in retrospect that we can believe in evolution.

IX. THE INSECT WINGS

The highest mechanical achievement of the arthropods is the power of flight, and the credit for this goes entirely to the pterygote insects. As flying animals the insects surpass both the birds and the bats, and in some ways they are superior to any flying machine yet invented.

Since the wings were already fully developed in the earliest winged insects of the fossil record, we do not know when or how the insects acquired their organs of flight, and hence we must be content with theories. There are at least three theories that we can choose from concerning the origin of insect wings. An idea once proposed is that the wings being flat folds of the body wall amply supplied with tracheae, were derived from tracheal gills, but this theory involves a too roundabout way of wing development. The presence of a tracheal respiratory system implies that the insects first lived on land and breathed air; then to acquire tracheal gills they had to live for a while in the water; and finally to convert the gills into wings they returned to the land.

According to another theory, that of Goldschmidt (1945), based on wing deformities in the fly *Drosophila*, the wings are homodynamous with legs. The front part of a wing, Goldschmidt says, is a leg, and the entire wing has been evolved from the dorsal and ventral lobes of a polychaete parapodium. Raw (1956) limits the wing origin to the dorsal lobe of the parapodium. This theory still invokes the old belief that the arthropods are descended from polychaete annelids, and it would seem to imply also that the insects are a direct offspring from the polychaetes, rather than a final product of arthropod evolution. Raw (1956) says of the parapodia "it is improbable that between the ancestral Polychaete and the Insect they ever ceased to be appendages moved by muscles." It must be observed, however, that the musculature of the worm moves the parapodia forward and backward, and that the up-and-down movement of an insect's wings

involves an entirely different type of musculature. Certainly the oldest known insects, which were Collembola, and the modern apterygotes are wingless, and there is no evidence that they ever possessed wings, though the parapodial theory of wing origin requires the assumption that the first insects were winged and that the modern apterygotes have secondarily lost their wings. In any case it is too great a strain on the imagination to visualize a worm flopping along out of the water with its parapodia until it was able to fly and become an insect. If such a thing happened once, why has it not recurred again during the last 200 million years, since polychaetes are still abundant?

The simplest and most reasonable theory of the origin of insect wings is that the wings were developed from paranotal lobes of the thorax after the insects, whatever their previous history, became

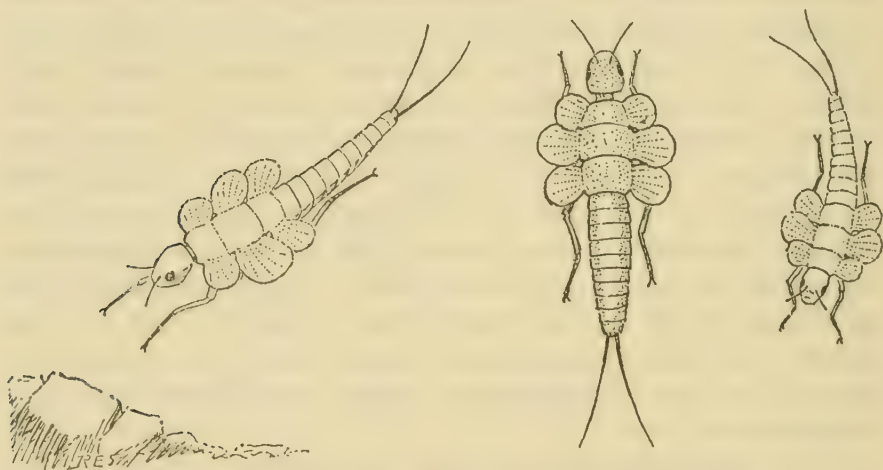


FIG. 22.—Insects in the glider stage of wing evolution.

terrestrial hexapods. Paranotal lobes are not hypothetical structures, since, as already shown, they occur in various modern arthropods, and in nonholometabolous insects the wings appear first on the nymph as lobelike extensions from the margins of the back plates of the mesothorax and metathorax. Presumably when paranotal lobes became sufficiently large in the primitive insects they first served as gliders (fig. 22). If the at first rigid paranotal lobes became flexible at their bases, they could then by action of thoracic muscles be flapped up and down and thus enable the gliding insect to sustain itself longer in the air. Even this simple wing movement, however, involved adaptive modifications of the thoracic skeleton, and some degree of adaptation in the musculature.

When the progenitors of the insects became hexapods by the elimination of functional legs from all but the first three segments behind the head, the thorax was thereby differentiated from the abdomen as the locomotor center of the body, and when wings were developed it is natural that they should be on the thorax alone.

As a prerequisite of wing movement by paranotal lobes, the thoracic walls, particularly the pleural areas, had to be strengthened to resist the stress of muscles that might operate the wings. Since evolution is not forward looking, it is not to be supposed that the thorax was prepared in advance for the role it was later to play in the wing mechanism. More probably, therefore, the pleural sclerotization of the thorax of winged insects was developed in the preglider stage to give stronger support to the legs. Before the insects could launch themselves as gliders from elevated positions they must have developed the habit of climbing, and for this they needed strong and well-supported legs. Later, the pleural plates gave support also to the paranotal lobes and finally to the wings. Hocking (1957) has made the interesting observation that, geologically speaking, the first winged insects appeared almost immediately with the appearance of tall plants growing from the swamps.

Clearly the development of wings from paranotal lobes was not a simple process of expanding the lobes, since it depended on previous modifications of the thoracic skeleton. The presence of strong pleural plates on the wingless prothorax of modern insects is further evidence that the thoracic pleura were first developed as leg supports. Since the development of wings took place after the insects became hexapods there is no reason to suppose that the abdominal segments ever had pleural plates like those of the thorax. The presence of well-sclerotized pleura on a winged segment, however, is essential to the wing mechanism. The pleural plates strengthen the side walls of the segment against the downward pull of vertical wing muscles, and each culminates in a fulcral process on which the wing rests and turns.

A paranotal lobe in order to become movable in the manner of a wing had to become first flexible on the notum mesad of its pleural support. It would thus be free to turn up and down on the pleural fulcrum. There would then be two principal ways in which the lobe or its wing derivative might be moved. The simplest method would be by the attachment of lateral body muscles on the wing base at opposite sides of the fulcrum. Muscles so attached acting as antagonists would elevate and depress the wings (fig. 23 B, C). This *direct* method of wing movement has been most efficiently developed by

the modern dragonflies. On the other hand, with the wings flexibly attached on the supporting notal plates mesad of the pleural fulcra, downward and upward movement of the notal plates (D, E) would give the wings the converse movements of elevation and depression. This *indirect* method of wing movement has been adopted by nearly all the flying insects except Odonata, but to give proper action to the

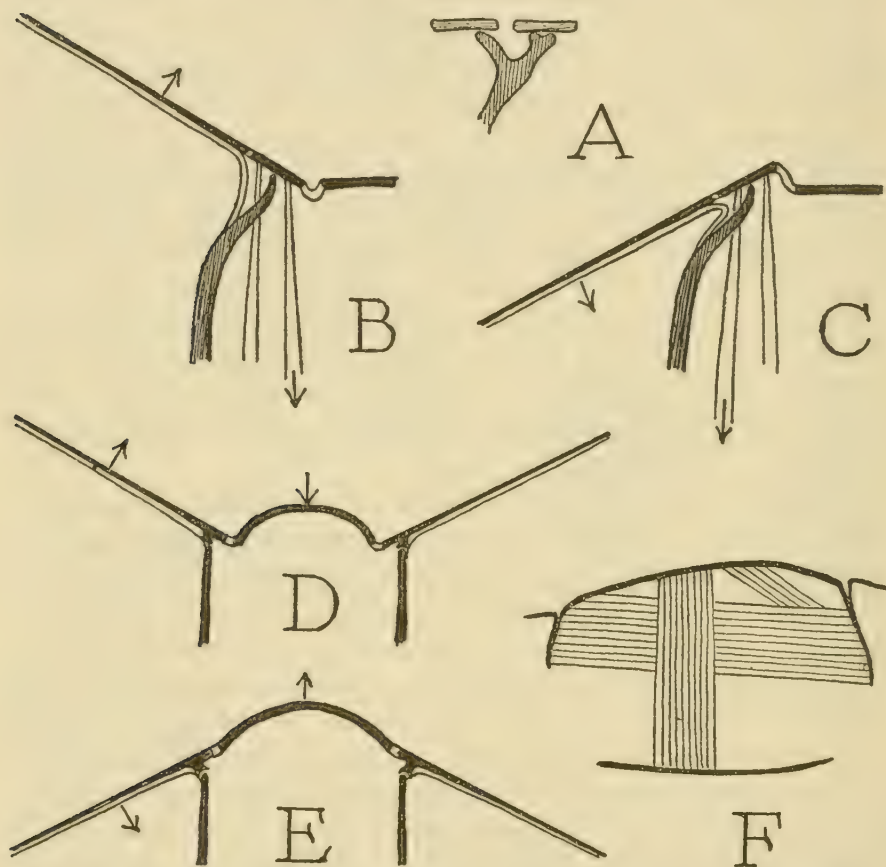


FIG. 23.—Diagrams of direct and indirect types of insect wing mechanism.

A, Forked pleural wing process of a dragonfly. B, C, Wing movements of a dragonfly by muscles attached on wing base at opposite sides of pleural fulcrum. D, E, Indirect type of wing beat by vertical movements of wing-supporting notal plate. F, The indirect flight muscles of a thoracic segment.

wing-bearing nota has involved reconstructive modifications in the thoracic skeleton and the development of an appropriate musculature. The wing mechanism of both the direct and indirect type will be more fully discussed later, but we should note here that the cockroaches and their relatives fly, rather inefficiently, by a mechanism somewhat intermediate between the other two.

The thoracic musculature of modern pterygote insects is so thoroughly adapted to the wing mechanism that it is difficult to visualize what may have been the pattern of the somatic musculature in primitive wingless insects. If the arthropods have been derived from annelid forebears, they probably, while still in a wormlike stage, had an outer layer of circular body muscles and inner bands of longitudinal muscles. With sclerotization of the back and venter, however, the segments could no longer be constricted, and the circular muscles were reduced to lateral muscles only. The somatic musculature of modern adult insects consists principally of longitudinal dorsal and ventral muscles and dorsoventral lateral muscles. In the thorax the lateral muscles have become diversified in their attachments, some being notosternal muscles, others notopleural, and still others notal or pleural leg muscles. When wings were developed, any of these muscles could serve as wing motors.

We might look to the modern apterygote insects for the primitive type of insect thoracic musculature. The apterygotes, as shown by Barlet (1950, 1953, 1954), have an elaborate thoracic musculature including dorsal muscles and numerous lateral muscles. In *Lepisma saccharina*, Barlet (1954) enumerates four muscles from the notum to the anapleurite in the mesothorax and five in the metathorax. In each of these segments he finds six notal muscles going to the catapleurite, and four to the trochanter. Pleural leg muscles include in each segment two muscles from the anapleurite to the coxa, and one to the trochanter, while another trochanteral muscle arises on the catapleurite. Likewise in a machilid Barlet (1950) shows that in the mesothorax numerous muscles arise on the notum and have various ventral attachments. It is clear, however, that the thoracic musculature of the apterygotes is adapted to the needs of these insects and could hardly serve as the basis for the wing musculature of the pterygotes. No apterygote could fly even if it had wings.

The dragonflies have made use of the lateral thoracic muscles for moving the wings. Since the dorsal walls of the paranotal lobes or the wing bases are lateral extensions of the notum, muscles here attached have simply retained their original notal connections. The problem of the early dragonflies then was to divide these muscles into two functional groups pulling on opposite sides of the wing fulcrum. The problem was readily solved by curving the wing fulcrum inward until it supported the wing base between lateral and mesal groups of the muscles (fig. 23 B). The muscles attached mesad of the fulcrum thus became wing elevators (B) and those laterad of it became wing depressors (C).

In modern Odonata the base of each wing contains two large sclerites that support the veins, an anterior *humeral plate* and a posterior *axillary plate*. The wing fulcrum, arising from a strong pleural ridge, bends inward, not into the thoracic cavity but in a fold of the subalar membrane, and forks into two arms, one to the humeral plate, the other to the axillary plate (fig. 23 A). Thus the muscles pulling alternately on opposite sides of the fulcral arms rock the wings up and down.

The thoracic musculature of the dragonflies has been described by Clark (1940), Marta Grandi (1947b), and several earlier writers. Most of the wing muscles are thick cylinders of fibers attached on the wing bases by stalked cup tendons. The odonate wing muscles are said by Clark to be individually comparable to those of other insects. This may be so, but certainly they are quite different in their relative development and in the part they play in the wing mechanism from those of any other modern insects. Dorsal longitudinal muscles are relatively small in the thorax of all Odonata; according to Grandi they are absent in the metathorax of Libellulidae. The horizontal or partial rotary component of the wing movements necessary to give forward flight is probably produced by anterior and posterior muscles attached on very small sclerites imbedded in the membranous pleural wall beneath the wings, which, as pointed out by Chao (1953), evidently represent the basalar and subalar sclerites of other insects. The mechanism of the dragonfly wings, however, has been less studied than the musculature. The thoracic structure has been modified in ways characteristic of the Odonata; the pleural sclerotization of the alate segments is confluent, producing a strong lateral wall on each side. The pleural ridges are greatly strengthened to withstand the double pull of the muscles on the wing bases. A comparative study of them made by Sargent (1937) shows that in the Aeschnidae the ridges are deep folds, which, particularly in the Gomphinae, take on a scalariform structure by the development of crossbars in the posterior walls.

It is clear that even in the dragonflies the paranotal lobes were not converted directly into organs of efficient flight; adaptational adjustments of the thorax, and reorganization of the muscles had to be evolved. Yet the thoracic structure of the dragonflies is simpler than that of insects with an indirect wing mechanism. If Lemche's (1940) classification of the Odonata and the extinct Protodonata with the Megasecoptera and Palaeodictyoptera is well founded, the direct method of wing movement may have been that of all these early insects, and probably was the first to be evolved.

Another insect group of ancient origin includes the cockroaches, the mantids, the termites, and probably the zorapterans, classed by Chopard (1949) as a superorder, the Blattopteroidea. These insects also make use of the dorsoventral muscles for wing motors, but not in the same way as do the dragonflies. The thoracic musculature of the cockroaches has been described by Carbonell (1947) in *Periplaneta* and by Tiegs (1955) in *Blattella*, that of the mantis by Leverault (1938), LaGreca and Raucci (1949), and Tiegs (1955), that of a winged termite by Fuller (1924). In these insects the dorsal longitudinal muscles are either absent or are too small to have any indirect action on the wings. The dorsal muscles are fairly large in Zoraptera, but have nothing like the size of the dorsal muscles of insects with an indirect flight mechanism. A relation of the Zoraptera to the Blattopteroidea, however, may be inferred from the thoracic structure, which, according to Adam and Lepointe (1948), is that of the cockroaches and mantids.

The method by which the blattopteroids move their wings is not well understood. Arising on the notum of each alate segment, however, are numerous muscles which are mostly leg muscles, though in the termites there are large notosternal and notopleural muscles. These muscles by depressing the notum might elevate the wings in the manner of the notosternal muscles of insects with a typical indirect flight mechanism. The downstroke of the wings, on the other hand, is probably produced by lateral muscles attached on basalar and subalar sclerites. The blattopteroids are relatively weak flyers, but they have advanced beyond the dragonflies in one respect, which is the development of a flexor apparatus in the base of each wing, by which the wings are folded horizontally backward when at rest.

Tiegs (1955) says of the Orthoptera that they are of primary importance in the evolution of the wing mechanism for the light they "can still throw on the initial adaptation of the thoracic musculature to flight." However, it is evident that the members of the blattopteroid group have made little progress, if any, toward the development of an indirect type of wing mechanism; rather, they seem to have a not very efficient type of mechanism of their own based somewhat on the dragonfly scheme of direct wing movement. There is no evidence that the dorsal musculature has been secondarily reduced, since structural features of the thorax that are essential to the indirect type of wing mechanism, such as postnotal plates between the wing-bearing plates and intersegmental phragmata, are entirely undeveloped. The cockroaches and the mantids very probably never flew better than they do today. The Blattopteroidea, on the basis of their

wing musculature and thoracic structure, are appropriately separated in classification from the rest of the orthopteroid insects.

The indirect mechanism of wing movement in which the up-and-down strokes are imparted to the wings by vibrations of the supporting notal plates is that made use of by all the winged insects except the Odonata and the Blattopteroidea. The upstroke results from the depression of the notum by notosternal or other vertical muscles; the downstroke is produced by the lengthwise compression and arching of the notum by contraction of the longitudinal dorsal muscles. Before this mechanism could be operative, however, several adaptive modifications had to be made in the thoracic skeleton, and the muscles involved had to be sufficiently enlarged to be effective.

The indirect elevator muscles of the wings are principally large notosternal muscles (fig. 23 F), though some of the dorsal muscles may become so oblique that they probably contribute to the depression of the notum. Comparable notosternal muscles are not generally present in insects having a direct wing mechanism. The notosternal muscles have been shown by Kelsey (1957) in the megalopteron *Corydalus* to originate in the pupa, having no counterparts in the larva. Holometabolous larvae, however, are metamorphosed forms, and their musculature, which usually is either reduced or elaborated, serves their own needs. The normal adult musculature is restored in the pupa.

The notal plates of wingless segments are ordinarily connected by so-called "intersegmental" membranes, and the dorsal muscles are attached on the intersegmental antecostae of the notal plates (fig. 24 A). To utilize these muscles as wing depressors, therefore, the membranous conjunctivae between the mesonotum and the metanotum, and between the metanotum and the first abdominal tergum had to be eliminated, otherwise the contraction of the muscles would simply pull the wing-bearing plates together without producing any deformation of these plates. To obviate this action, the intersegmental membranes behind the wing-bearing nota have become sclerotized, forming plates that brace each wing-bearing plate against the one behind it (B). The dorsum of each winged segment thus typically contains an anterior wing-bearing *notal plate* (*N*) and a posterior *postnotal plate* (*PN*). The contraction of the dorsal muscles can now arch the nota upward and thus deflect the wings on the pleural fulcra. To accomplish this effect, however, the dorsal muscles must be greatly enlarged, and to accommodate their increase in size the antecostae (*Ac*) on which they are attached have been produced

into deep sclerotic folds, or *phragmata* (C, *Ph*). Most insects that fly with both pairs of wings have a prothragma on the anterior margin of the mesonotum, a middle phragma on the mesothoracic postnotum, and a posterior phragma on the metathoracic postnotum. The three phragmata, however, are actually intersegmental in position.

Finally, the indirect flight muscles themselves have undergone a structural change in the higher insects to give them increased strength

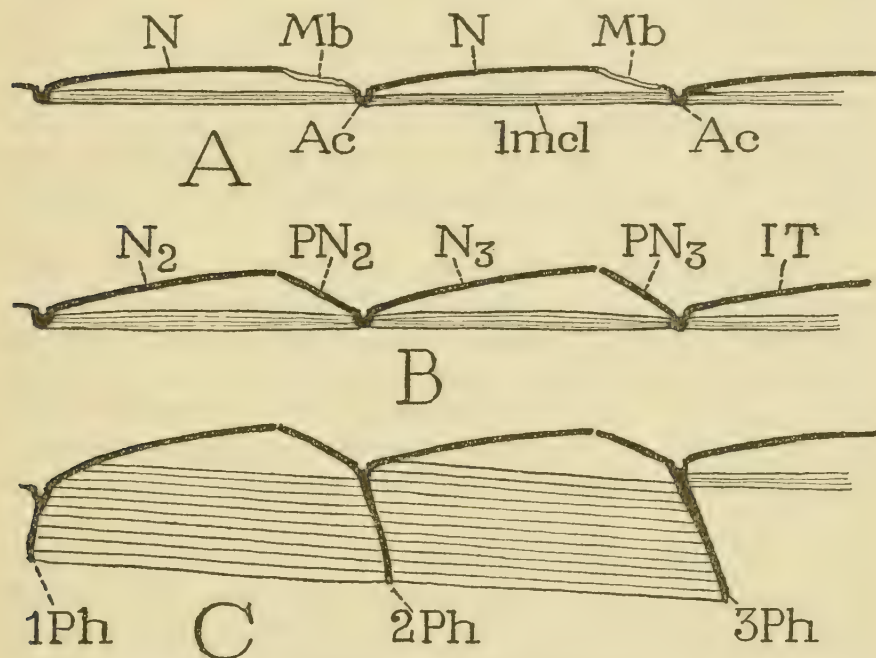


FIG. 24.—Development of postnotal plates and phragmata in the evolution of the indirect type of insect wing mechanism.

A, Section through consecutive notal plates with generalized structure, nota connected by infolding membranes. B, Internotal membranes of winged segments replaced by sclerotized postnotal plates. C, Development of phragmata from the intersegmental antecostae to accommodate increased size of dorsal muscles.

and speed of contraction. The ordinary muscles of insects have the usual muscle structure in which the fibers are composed of extremely fine fibrillae less than half a micron in section. In the higher orders the fibrils of the indirect flight muscles are greatly thickened, distinctly striated sarcostyles that may be as much as five microns in diameter. The sarcostyles are separated by spaces containing numerous large mitochondrial bodies known as *sarcosomes*, and are readily teased apart by ordinary dissection. The number and size of the

sarcosomes is closely related to the increased physiological activity of the flight muscles.

The first efforts of the insects to fly by flapping the primitive wings up and down could have accomplished little more than a lifting of the insects in the air. To give forward or directed flight the wings must have a partial rotary motion on their long axes accompanying the vertical movements. Probably some rotary movement resulted automatically from air pressure and the nature of the wing articulation on the body, but it became mechanically controlled with the attachment of strong lateral muscles on movable epipleural basalar and subalar sclerites in the membrane beneath the wing bases before and behind the wing fulcra. That the basalar and subalar sclerites are secondary differentiations of the upper part of the pleuron is clear from the work of Kelsey (1957) on *Corydalus*. Most insects with an indirect flight mechanism have a wing-flexing apparatus like that of the Blattopteroidea.

It is evident that the acquisition of an efficient indirect flight mechanism has not been a simple matter of direct evolution of paranotal lobes into wings. As finally developed, however, it has made the insects unsurpassed flying machines. According to the records of Sotavalta (1947) certain dipterous midges have a wing-beat rate of 800 to 1,000 per second. By contrast, the strong-flying dragonflies with their direct wing mechanism make only 35 to 52 wing beats per second.

In some of the higher insects there are a number of small muscles attached on the axillary sclerites of the wing base. Such muscles have been described by Williams and Williams (1943) and by Zalokar (1947) in *Drosophila*, in which muscles from the pleuron go to the first, third, and fourth axillaries. These muscles are termed "wing adjustors" by Tiegs (1955), their function being to adjust the position of the axillaries to steering movements of the wings. In a tipulid he finds three small muscles attached on the axillaries and other parts of the wing base, besides four from the pleural arm and the episternum attached on the notum and two below the wing. Observations on the presence of these muscles in other insects are not extensive. Ritter (1911) describes a pleural muscle of the first axillary, and two others attached on the anal ligament in the wing of a blow fly; Mihalyi (1935-36) mentions no axillary muscles in the house fly.

Among the axillary muscles the most important is the pleural muscle of the third axillary that operates the flexing apparatus by

which the wing of most insects with an indirect motor mechanism is turned horizontally backward over the abdomen when not in use.

The first insects to adopt the indirect mechanism of wing movement must have been the ancestors of the modern Ephemeroptera, or mayflies. The thoracic pleural sclerotization is yet imperfectly developed in the mayflies, but it includes a wing fulcrum and differentiated basalar and subalar plates. In the axillary region of the wing are several small sclerites termed by Grandi (1947a) pseudopteralia, but Matsuda (1956) says the wing-base sclerites of *Siphonurus* closely correspond with the usual three axillaries of other insects. There is, however, no wing-flexing apparatus, the wings being usually held vertically over the back when at rest. Both Grandi and Matsuda have fully described the wing musculature of the Ephemeroptera; discrepancies in the two accounts are unimportant. The wing motors include large longitudinal and oblique dorsal muscles, a pair of thick notosternal muscles, and perhaps a nototrochantinal muscle. The wing mechanism of the mayflies is thus clearly of the indirect type, in striking contrast to that of the dragonflies. The Ephemeroptera and the Odonata, therefore, are not related insects; they represent two early lines of pterygote evolution differentiated by the method adopted for moving the wings.

The flight of the mayflies is weak and the principal movements of the wings are up and down. Since adult mayflies have no functional feeding organs, as noted by Edmunds and Traver (1954), they have no concern with food finding, and the only use of their wings is for mating flight. "The nuptial flight of most mayflies," these writers say, "consists of flying upward and then passively coasting or leisurely flying downward." The mayflies, both larvae and adults, show by many structural features that they are relatively primitive pterygotes, but their relation to the higher insects with an indirect wing mechanism is not clear.

The Plecoptera have a strongly developed indirect wing mechanism. In *Perla*, as described by Grandi (1948) and by Wittig (1955), there are huge longitudinal and oblique dorsal muscles in each winged segment, and a pair of large notosternal muscles. Other notal muscles include muscles from the pleuron, the furcisternum, and the coxae.

Among the orthopteroid insects the wing mechanism of Gryllidae, Tettigoniidae, and Acrididae is of the indirect type. The flight muscles are relatively weak in the first two families, but they attain a high degree of development in the strong-flying acridids (see Snodgrass, 1929; Misra, 1947; Albrecht, 1953; Tiegs, 1955). In short-

winged or wingless species the musculature evidently has undergone a secondary reduction. *Grylloblatta* is an entirely wingless insect, but its relation to winged Orthoptera leaves little doubt that it once had wings. It still retains relatively large longitudinal and oblique dorsal muscles in both the mesothorax and the metathorax, but the size of these muscles, Walker (1938) points out, is related to the free mobility of the thoracic segments on each other. With the absence of wings, however, is associated a complete absence of notosternal muscles. In orders in which all species are wingless, as Mallophaga (Mayer, 1954) and Siphonaptera, the dorsal muscles are small.

From the Orthoptera on through all the higher orders of insects that have functional wings, including Megaloptera (Kelsey, 1957), Neuroptera (Czihak, 1956), Psocoptera (Badonnel, 1934, fig. 45), the standard wing mechanism is that of the indirect type, which clearly has proved to be highly efficient for swift and controlled flight. The direct mechanism as developed by the dragonflies, however, is hardly to be rated as inferior to the indirect mechanism. The two ways of flying were not evolved by competition; they were simply adopted from the beginning as two possible ways of moving the wings. The dragonflies came from a group of primitive insects that have left no descendants other than modern dragonflies; the inventors of the indirect flight mechanism account for most of the other insects in the world today. As noted by Hocking (1957) the insects during their experimental and developmental stages of wing evolution for nearly 100 million years had the air to themselves free from attack by other flying creatures. Then when the birds and the bats came along the poorer models were the first to be eliminated.

Even after the indirect wing mechanism had attained a high degree of efficiency for flight, certain other improvements and accessories have been added. Most insects move the two wings on each side in unison, and in general it seems there is a tendency to reduce the size of the hind wings. Unity of movement has been better secured in some cases by linking the smaller hind wings to the fore wings, as in Lepidoptera and bees. This has resulted in an economy in the motor apparatus by allowing a reduction of the metathorax and its muscles as the mesothorax takes over the chief function of moving both pairs of connected wings. The Diptera have attained the ultimate in two-winged flight by completely eliminating the hind wings as organs of flight and highly developing the mesothorax and its muscles to motorize the single pair of wings.

The hind wings of the Diptera, however, have not been discarded as useless, but have been converted into important regulatory organs of the flight mechanism. They are reduced to club-shaped or capitate rods with enlarged bases, and during flight they vibrate in a vertical plane at the same speed as the wings but in opposite phase. The organs are called *halteres* because they were formerly regarded as balancers, but to express their function as it is now known Fraenkel and Pringle (1938) have termed them "gyroscopic organs of equilibrium." Removal of the halteres from a live fly results in a complete loss of flight control, particularly when the fly attempts to rotate about a vertical axis.

The base of each halter is equipped with numerous proprioceptive sense organs, including several groups of campaniform organs and chordotonal organs. The sensilla on the halteres of Diptera were minutely studied by Pflugstaedt (1912), and his account has been fully verified by Pringle (1948), who closely analyzed the operation of the halteres as flight stabilizers. When the insect on the wing alters the direction of its flight, the change produces stresses in the bases of the vibrating halteres, which will be registered in one group or another of the basal sense organs. Specific nerve impulses are thus delivered to the nerve centers of flight, which enable the insect to give the proper motor response to maintain its equilibrium in the air.

There is little question that the ancestors of the Diptera were four-winged insects, and there must have been some advantage in the change to the two-wing condition by reducing the hind wings. It is evident, however, that during the change the flies were not able to adapt to two-wing flight without a stabilizer apparatus. It therefore poses a problem in evolution to understand how the hind wings were reduced to halteres and at the same time became instruments for stabilizing flight by the fore wings. It is to be noted, however, that the wing bases themselves contain the same kind of sense organs as those of the halteres; the regulatory action of these sense organs, therefore, is not a newly acquired function.

Finally, there are the so-called veins of the wings, which, being strengthening ribs, must be of importance in the wing mechanism. The vein arrangement is characteristic of orders and differs even among genera and species, and a study of wing venation has been a major part of the work of insect taxonomists. On the other hand, little attention has been given to the functional significance of the numerous venational patterns.

ABBREVIATIONS ON THE FIGURES

- Ac*, antecosta.
An, anus.
Ant, antenna (1*Ant*, first antenna, 2*Ant*, second antenna).
Ap, apodeme.
Apl, anapleurite.
art, articulation.

Ba, basalar.
BC, body cavity.
bcg, branchiocardiac groove.
brc, branchial chamber.
Brn, branchia (gill).
Brnstg, branchiostegite.
Bspd, basipodite.

Chl, chelicera.
cmcls, compressor muscles.
Cp, carapace.
Cpl, catapleurite.
Crppd, carpopodite.
Cx, coxa.
CxC, coxal cavity.
CxP, pleural coxal process.
Cxpd, coxopodite (coxa).

D, dorsum.
Dactpd, dactylopodite.
DbI, doublure.
dImcl, dilator muscle.

E, compound eye.
emH, embryonic head (cephalic lobe).
Endpd, endopodite.
Endst, endosternum.
Endt, endite.
Epm, epimeron.
Eppd, epipodite.
Eps, episternum.
Expd, exopodite.

Fm, femur (meropodite).

Gn, gnathal tagma.

Hphy, hypopharynx.

imH, imaginal head.
isMb, intersegmental membrane.

J, leg joint.

L, leg.
Lcx, lamina coxalis.
Lg, intergnathal ligament.
Lm, labrum.
lmcl, longitudinal muscle.
ltg, laterotergite.

Mb, "intersegmental" membrane.
Md, mandible.
Mrpd, meropodite (femur).
Mts, metazonite.
Mxpd, maxilliped.

N, notum (*N*₁ pronotum; *N*₂, mesonotum; *N*₃, metanotum).

Ostg, oostegite.

Pat, patella.
Pdp, pedipalp.
Pgn, paragnath.
Ph, phragma (1*Ph*, 2*Ph*, 3*Ph*, first, second, third phragma).
Pl, pleuron.
pl, pleurite.
plAp, pleural apodeme.
plMb, pleural membrane.
PLR, pleural ridge.
pmcl, protractor muscle.
PN, postnotum.
pnl, paranotal lobe.
Propd, propodite.
Prtc, protocephalon.
Prz, prozonite.
Ptar, pretarsus (dactylopodite).

R, rostrum.
Rd, posterior reduplication.
rmcl, retractor muscle.

S, sternum.
Sa, subalar.
sAp, sternal apodeme.
Scx, subcoxa.

<i>Seg</i> , leg segment.	<i>Tr</i> , trochanter (<i>1Tr</i> , first trochanter
<i>Sp</i> , spiracle.	<i>2Tr</i> , second trochanter, or pre-
<i>Stom</i> , stomodaeum.	femur).
	<i>Tra</i> , trachea.
<i>T</i> , tergum (notum).	
<i>Tar</i> , tarsus.	<i>V</i> , venter.
<i>Tb</i> , tibia.	<i>vmcls</i> , ventral muscles.
<i>Tlpd</i> , telopodite.	
<i>Tn</i> , trochantin.	<i>WP</i> , <i>wP</i> , pleural wing process.

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LONG-RANGE WEATHER FORECASTING

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LONG-RANGE WEATHER FORECASTING

By C. G. ABBOT

Research Associate, Smithsonian Institution

Weather comprises departures from climate, which represents the average march of weather conditions over long intervals.

For purposes of my long-range forecasting, weather falls into three classes:

A. Weather of this half-century separated from that of the next preceding.

B. Weather attending high sunspot activity separated from that attending low.

C. Weather influenced by different seasons of the year, separately tabulated.

Subject to these separations, precipitation and temperature at all stations, and in all times within the past century, and probably for many years to come, are determined in their principal trends by one family of periods, which are exact submultiples of 273 months.

About 70 harmonics belonging to this family are known to be occurring in one or another of several kinds of phenomena. For purposes of long-range weather forecasting 27 of these periods are sufficient. By using them correctly, forecasts and backcasts for as much as 60 years have resulted successfully.

No data other than records of monthly mean weather observations and Wolf sunspot numbers for the past century are required for these forecasts or backcasts.

Table 1 gives the 27 periods employed. They are tabulated as fractions of 273 months and as periods in months and fractions thereof.

One thousand months or more of consecutive records are to be employed. The following groups are made for forecasting:

As regards seasons: January to April; May to August; September to December.

As regards sunspot activity: Wolf numbers less than 20; Wolf numbers above 20.

As regards secular time: Years of the first half of the record; years of the second half.

With this grouping, approximately 1,000 months of records will be divided into 220 groups. Many groups will therefore contain too few columns in tabulation to give trustworthy means. To remedy this difficulty, I combine six groups into one, by shifting phases to agreement and taking a general mean. I make such combinations for all periods up to $15\frac{1}{6}$ months, throwing records with sunspots less than 20 Wolf numbers into one combination, and those above 20 into another. For periods above $15\frac{1}{6}$ months I forego division for the three periods of the year. When using the combined forms in forecasting they must be used in the original phases of constituents. These arrangements for the shorter periods are illustrated by figure 1.

By the process just described and illustrated in the figure, one greatly reduces below 220 the actual number of mean forms and amplitudes to be combined in making a forecast from 27 periods. But when using the combined mean forms described, one must readjust their phases to the phases their constituent parts had originally. Besides this fruitful source of mistakes, one must be careful to apply correctly at the proper intervals allowances to take care of the fractional parts of months found in 24 of the 27 periods of table 1, and must also regard plus and minus signs.

Details of my method of long-range weather forecasting are extensively published in the *Journal of Solar Energy and Engineering*, vol. 2, No. 1, January 1958. I shall confine the remainder of this paper to evidences that support the validity of the method and the soundness of its results.

1. *The exact master period or fundamental is 273 months.*

This period (within existing uncertainty) is double the well-known "sunspot period" of $11\frac{3}{8}$ months. It is also associated with Hale's magnetic period in sunspots. Having discovered that approximately $10\frac{1}{2}$ months is a strong period in Washington precipitation, I determined its amplitude for several periods differing slightly from $10\frac{1}{2}$ months. For this purpose I used about 790 monthly mean values of Washington precipitation, all observed when Wolf sunspot numbers exceeded 20. The values were smoothed by 3-month consecutive means, which of course reduces the ranges of percentage departures from normal to about two-thirds of their actual monthly values. Table 2 and figure 2 show the results.

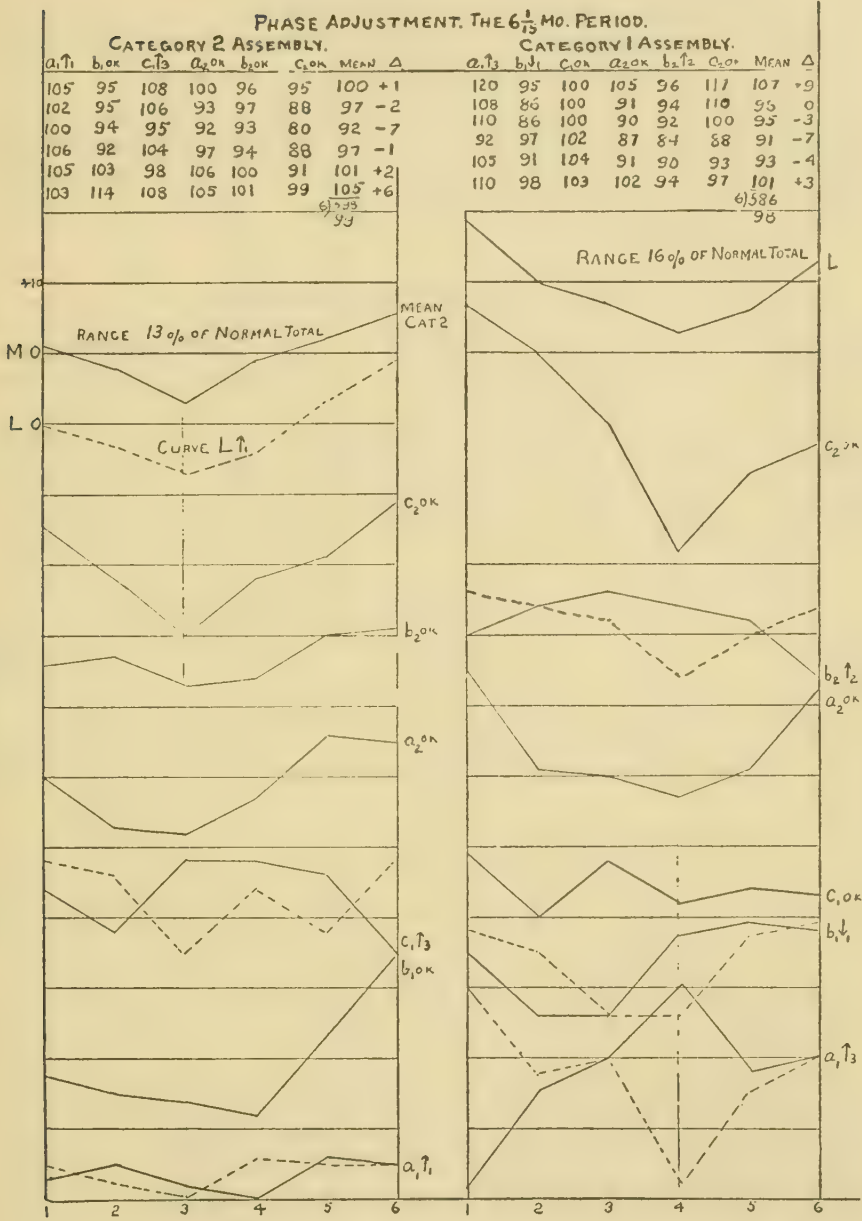


FIG. 1.—Sixfold combinations of weather periods.

The irregularities of run are naturally caused by irregularities in the rainfall from month to month. The phases of the 4 periods differ, of course, because the periods are unequal.

Figure 2 clearly shows that a value of the master period between 273 and 275 months is definitely indicated.

I have preferred 273 months rather than 275 months because it is an integral multiple of the strong periods 7, 13, 39, and 91 months. It cannot be much more than one-third percent from the true master period.

TABLE I.—*Harmonics of 273 months*

Fractions of 273...	1/3	1/4	1/5	1/6	1/7	1/8	1/9	1/10	1/11
Length in months..	91	68-1/4	54-3/5	45-1/2	39	34-1/8	30-1/3	27-3/10	24-9/11
Fractions of 273...	1/12	1/14	1/15	1/18	1/20	1/21	1/22	1/24	1/26
Length in months..	22-3/4	9-1/2	18-1/5	15-1/6	13-13/20	13	12-9/22	11-3/8	10-1/2
Fractions of 273...	1/27	1/28	1/30	1/33	1/36	1/39	1/45	1/54	1/63
Length in months..	10-1/9	9-3/4	9-1/10	8-3/11	7-7/12	7	6-1/15	5-1/18	4-1/3

TABLE 2.—*Percentage amplitudes of proposed periods*

Period Months	Percentage runs										Ranges Percent
$\frac{271.2}{27}$	105.7	103.4	102.5	100.7	100.9	96.3	97.3	97.9	98.0	97.7	9.4
$\frac{273.0}{27}$	95.7	95.8	93.4	96.1	99.3	102.0	103.7	108.0	104.8	101.1	14.6
$\frac{275.0}{27}$	109.8	102.4	103.3	99.3	95.4	92.9	96.2	97.6	98.8	104.5	16.9
$\frac{277.0}{27}$	94.6	104.4	106.2	101.3	105.8	105.5	194.6	97.5	96.9	93.3	12.9

2. All discovered periods in weather are integrally related to 273 months.

As to periods greater than 273 months: About 1936 I pointed out that the fluctuations of level of the Great Lakes indicated periods of severe drought in the Northwest following 1837, 1885, and 1929. Lesser droughts occurred about halfway between these dates. Knowing the solar period of about $22\frac{3}{4}$ years, I predicted drought in the decades 1950-60, 1975-1985, 2000-2010, and 2020-2030. The drought following 1952 has already occurred. Though more severe than I expected, it ended in 1957, lasting only half as long as the great depressions of the Lakes following 1837, 1885, and 1929.

Exact evidence on the lengths of the periods less than 273 months is at hand. When one tabulates monthly precipitation values to discover the forms and amplitudes of periods ranging in length from $15\frac{1}{6}$ to 91 months, the direct tabulations often show no convincing evidence

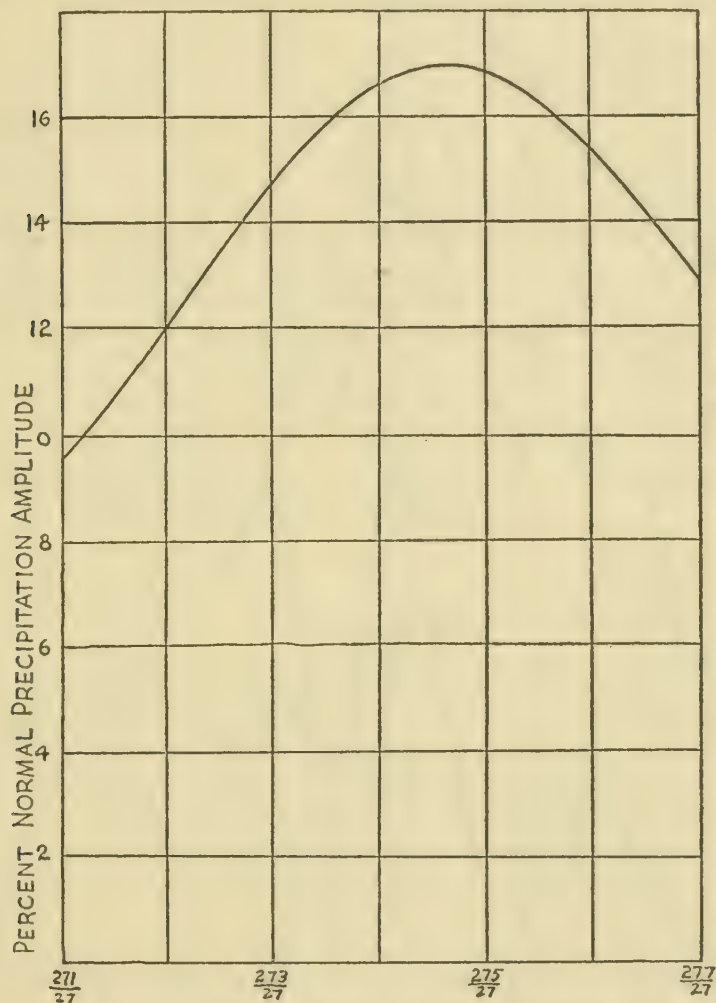


FIG. 2.—Length of the master period in weather.

that such periods exist, for the forms of these periods as shown in graphs have great excrescences which totally obscure the periods sought. These excrescences are caused by the superposition of one or more shorter periods integrally related to the one sought, and which must first be eliminated before the longer period appears.

Figures 3 and 4 give examples of this difficulty. Concerning fig-

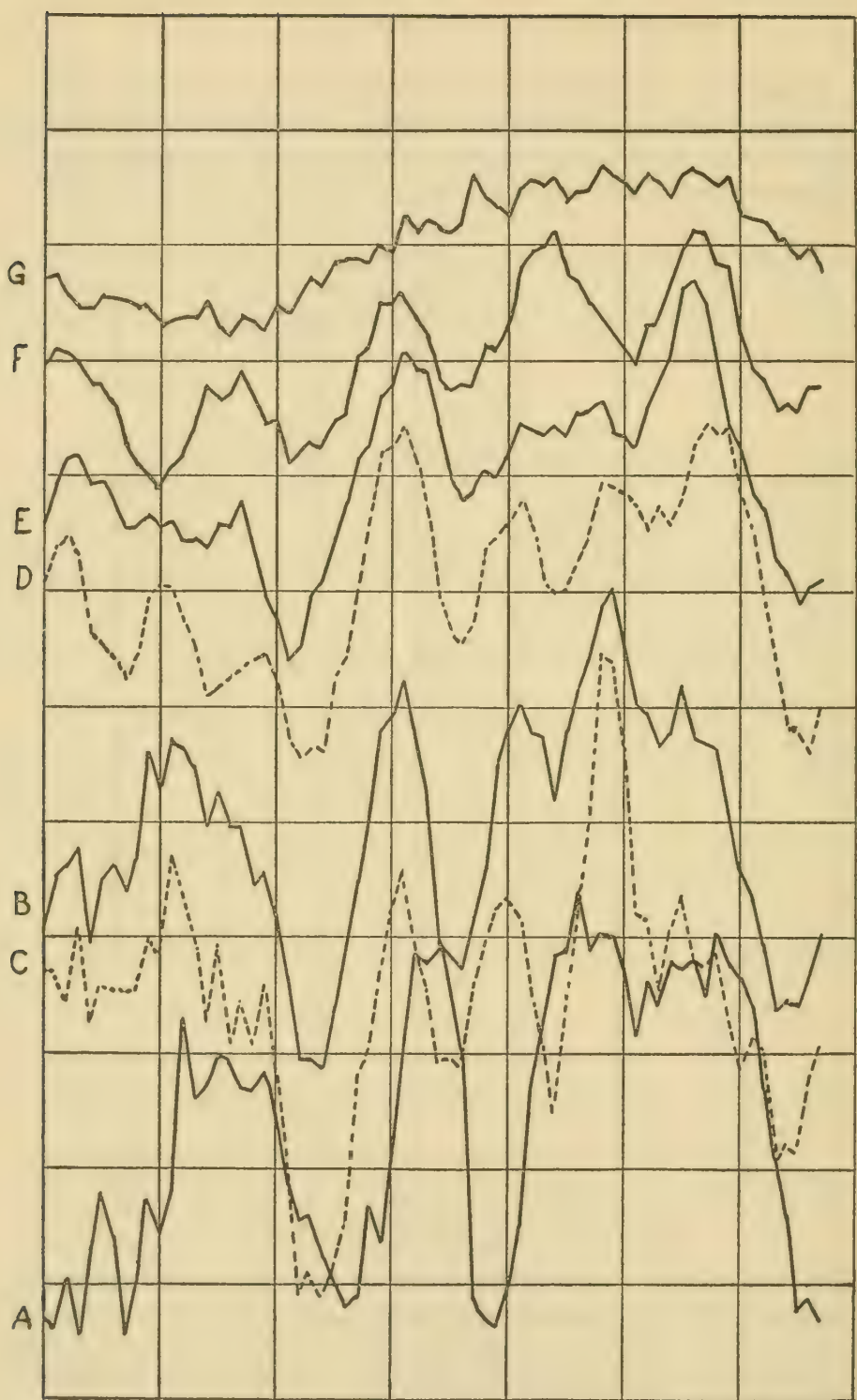


FIG. 3.—The 68½-month period in St. Louis precipitation cleared of shorter integrally related periods.

ure 3, I quote from my paper (Journ. Solar Energy and Eng., vol. 2, No. 1, p. 32), already cited.

As a graphical illustration, I reproduce here as figure 3, figure 9 of my paper "Sixty-year Weather Forecasts."¹ It represents the clearance of the $68\frac{1}{2}$ -month period in St. Louis precipitation. A and B are mean curves, A of 8 repetitions prior to 1900, and B of 7 repetitions subsequent to 1900. The phase of A appears to be 3 months later than the phase of B. Moving A back 3 months and taking the mean of the two, curve C results. This shows plainly the presence of a period of $\frac{1}{3}$ of $68\frac{1}{2}$ months. Obtaining its average form and amplitude and subtracting from curve C, curve D is obtained. Curve D presents 7 humps of about equal length. Taking their mean form and amplitude and subtracting, curve E remains. In curve E halves are clearly indicated, though not exclusively. Evaluating the average half and subtracting, curve F appears. And now obviously there remains a regular period of $\frac{1}{5}$ of $68\frac{1}{2}$ months. Evaluating and subtracting, we find curve G, which well represents the $68\frac{1}{2}$ -month period sought. Its range is 13 percent of St. Louis normal precipitation. This single diagram presents five members of the family related integrally to 273 months. These are $\frac{1}{4}$, $\frac{1}{8}$, $\frac{1}{12}$, $\frac{1}{20}$, and $\frac{1}{28}$ of 273 months.

Concerning figure 4, I continue quoting from the paper just cited, pages 32 and 33.

In figure 4 are given the results and details of the removal of overriding periods from the curve of the period of $45\frac{1}{2}$ months in the precipitation at Natural Bridge, Arizona, for $SS^2 < 20$, between the years 1890 and 1920. In curve A_1 are the average values of the precipitation for all repetitions of the $45\frac{1}{2}$ -month period when $SS < 20$. Curve Δ_1 remains after the removal of the average ordinates of the period $(45\frac{1}{2})/4$ months. Curve Δ_2 is what remains after removing from curve Δ_1 $(45\frac{1}{2})/6$ months. Curve Δ_3 remains after removing $(45\frac{1}{2})/7$ months. Curve Δ_4 remains after removing $(45\frac{1}{2})/5$ months. Curve Δ_5 remains after removing $(45\frac{1}{2})/3$ months, and it shows approximately the true form of the $45\frac{1}{2}$ -month period. The amplitude of the smooth curve through curve Δ_5 is 21 percent of normal precipitation at Natural Bridge. The reader should understand that in three other cases the $45\frac{1}{2}$ -month period was similarly cleared of overrides. These cases are for $SS < 20$, in the years 1921 to 1950; for $SS > 20$, between 1890 and 1920; and for $SS > 20$ from 1921 to 1950. So this one period, $45\frac{1}{2}$ months, involved much thought and

¹ Smithsonian Misc. Coll., vol. 128, No. 3, Publ. 4211, 1955.

² SS is my abbreviation for Sunspot number.

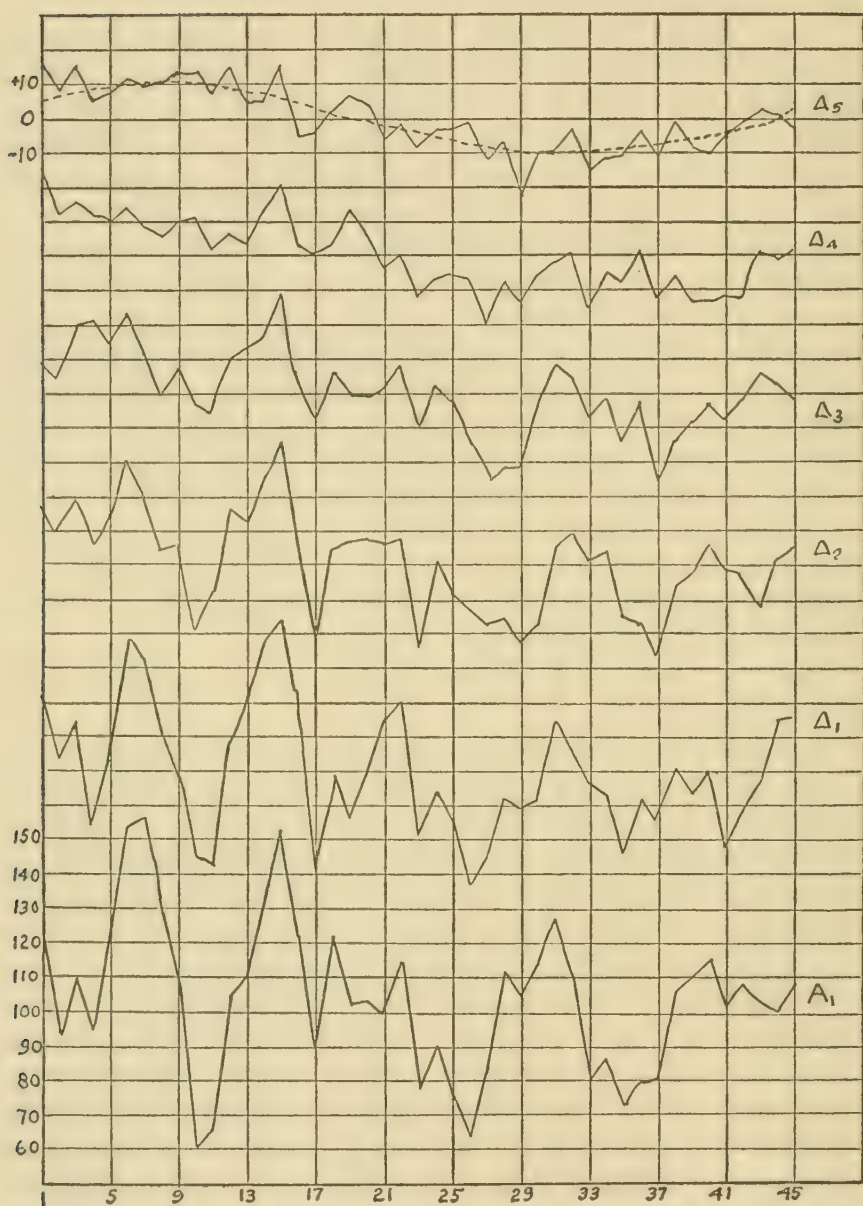


FIG. 4.—The 45½-month period in Natural Bridge precipitation, between 1890 and 1920, for intervals of Wolf numbers below 20, cleared of shorter integrally related periods.

work, requiring three additional treatments similar to figure 4. All the periods above 22 months in length required them also.

Merely referring to the two examples given above, of the clearing of overriders of lesser length integrally related to the original periodic curves, the reader has proof that not less than 11 integral submultiples of 273 months exist as regular periods in precipitation. Those discovered in figures 3 and 4 are $\frac{1}{4}$, $\frac{1}{6}$, $\frac{1}{8}$, $\frac{1}{12}$, $\frac{1}{18}$, $\frac{1}{20}$, $\frac{1}{24}$, $\frac{1}{28}$, $\frac{1}{30}$, $\frac{1}{36}$, and $\frac{1}{42}$ of 273 months. Their ranges in no case are less than 10 percent of normal precipitation. Yet all of them are unrecognized by meteorologists.

Besides these evidences I have in my records hundreds of similar examples which prove unquestionably that all of the 27 periods in weather named in table 1 are exact integral submultiples of 273 months. Not only so, but I have many similar examples from other fields of research which prove that not only these 27 weather periods but many others are exact submultiples of 273 months.

I suggest to students of hydrodynamics that this family may be a fruitful field for mathematical research in its relation to solar variations and weather.

3. *Approximately sine forms of the longer periods in precipitation.*

Not only do the curves of the sun's variation representing the family integrally related to 273 months approximate to sine curves, notwithstanding their large accidental errors compared to their small percentage range, but also the longer weather periods in precipitation and temperature, when cleared of integrally related shorter periods, are closely like sine forms.

Figure 5 is taken from my paper "Periodic Solar Variation."³ Though none of the curves of variation in the solar-constant measures shown in that figure exceeds 0.25 percent of the solar constant in amplitude, 20 of the 26 curves are well represented by smooth curves of nearly simple sine form.

In figure 6 I show some of the longer periods in precipitation for several weather stations, first as given by direct tabulation from the weather records, second after the removal of overriding shorter periods integrally related, and third by smooth curves following the forms of the cleared originals. The approximate sine forms are apparent in the end results, though quite impossible to descry in the original tabulations.

³ Smithsonian Misc. Coll., vol. 18, No. 4, Publ. 4213, fig. 3, 1955.

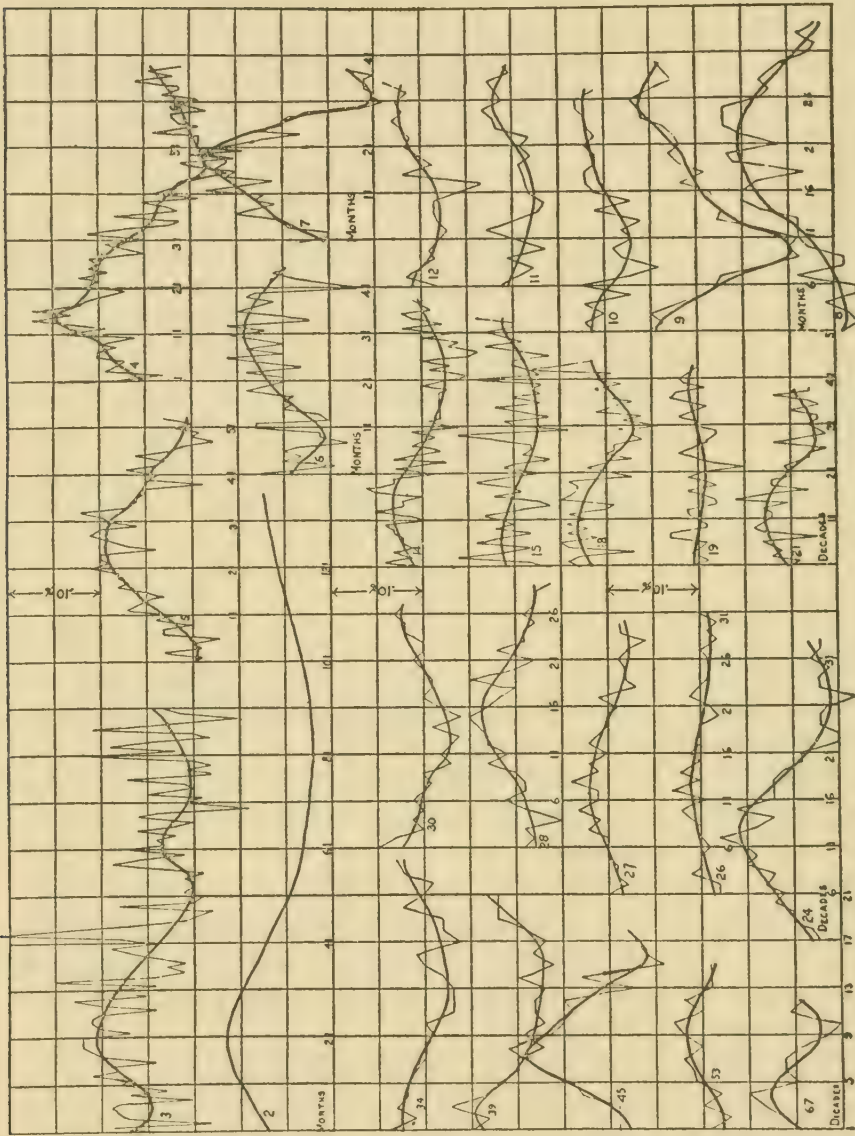


FIG. 5.—Twenty-six periods in solar variation, ranging from 4.08 months in 136½ months, as cleared of subordinate interfering integrally related periods.

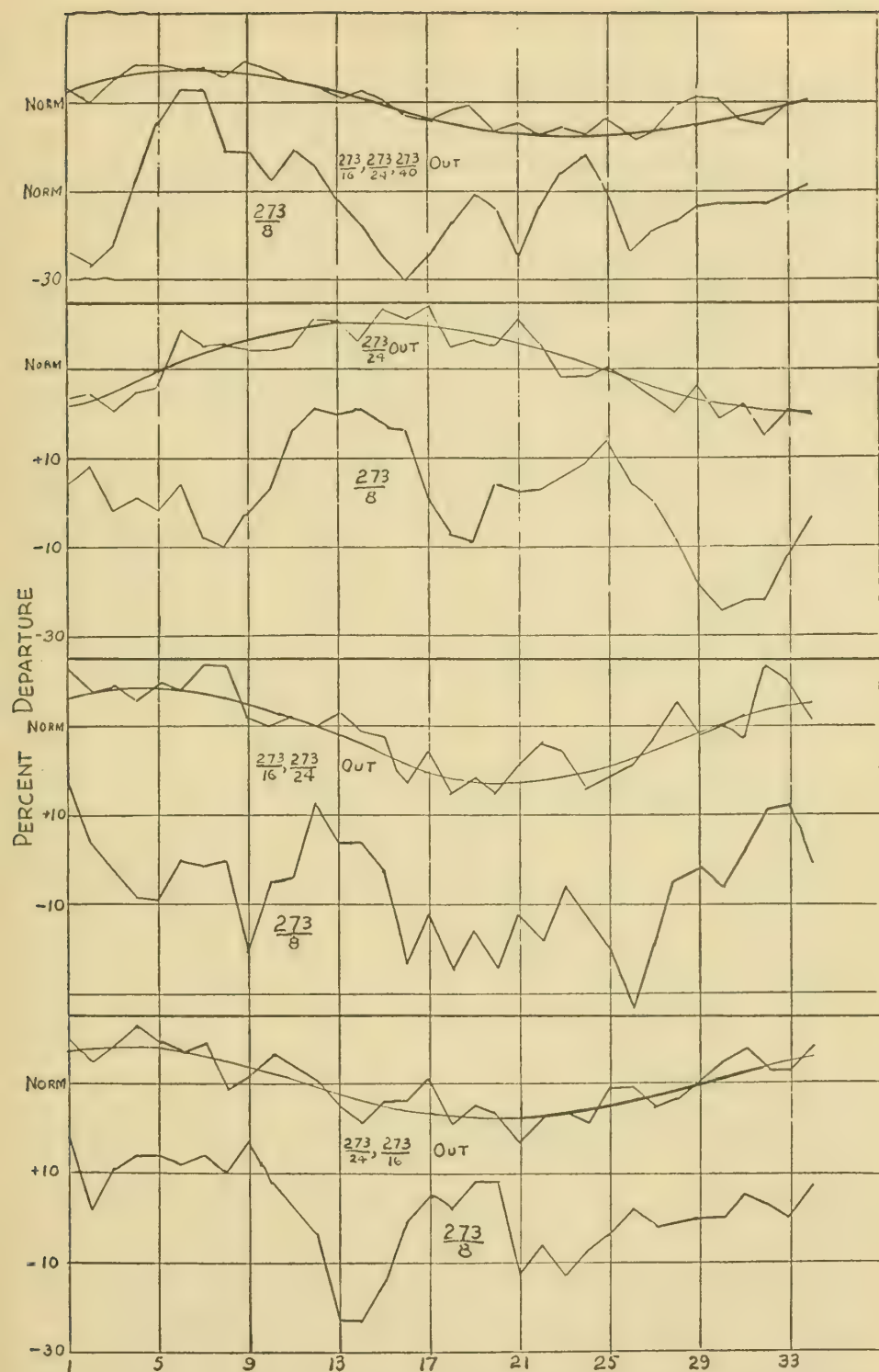


FIG. 6a.—Periods in precipitation as computed and as cleared of superposed integrally related shorter periods.

4. *Inequality of periodic amplitudes.*

A curious observation has presented itself which may have some bearing on any theoretical treatment of the problem of identity of the families of periods related to 273 months found in the solar varia-

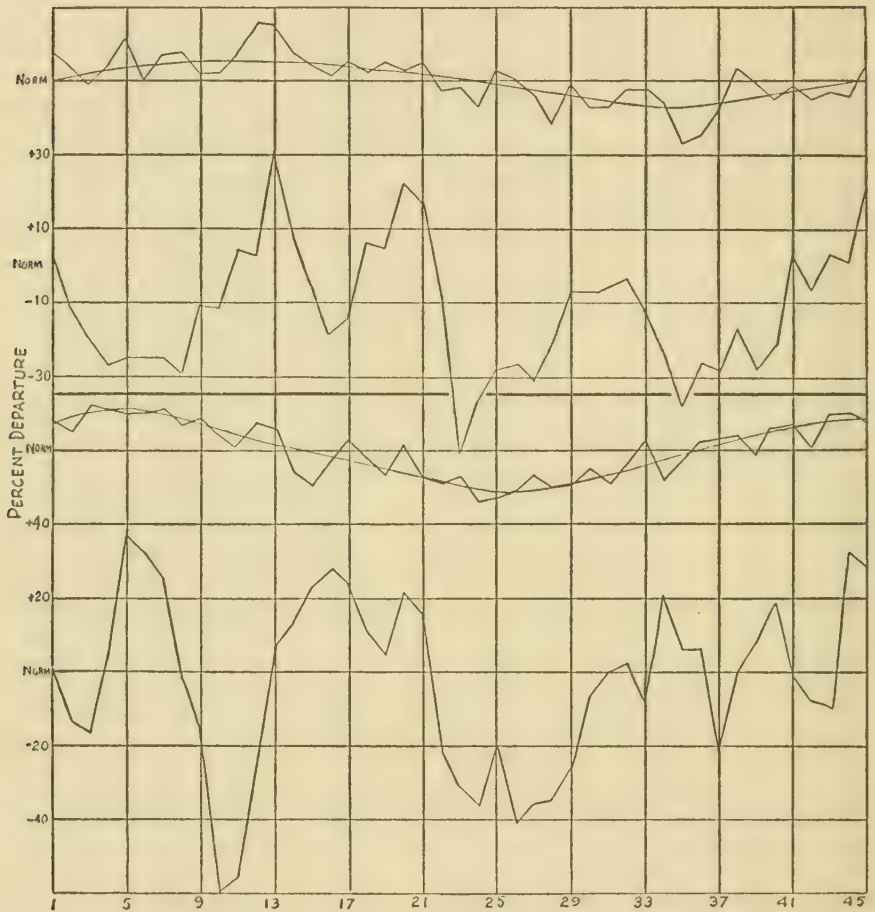


FIG. 6b.—Periods in precipitation as computed and as cleared of superposed integrally related shorter periods.

tion, the weather, and in other fields. The observation I refer to is this:

A great majority of the scores of periods I have determined for various cities, at times of sunspot numbers less than 20 Wolf numbers, exceed considerably in amplitude the corresponding periods in the weather of these cities as investigated for times of Wolf numbers exceeding 20. Table 3 gives a sample of such excesses.

5. *Weather trends may be well forecasted or backcasted for many years forward or backward.*

I have given above some hints about forecasting from the average background found in a thousand months, if used together with the knowledge of a family of periods integrally related to 273 months. Details of the method are given in the paper cited above. Since that paper was prepared, much additional experience has led to slight

TABLE 3.—*Percentage amplitudes of total normal precipitation of periods compared, for first half and second half of years of records, and for Wolf sunspot numbers greater and less than 20*

A. Mean precipitation, St. Louis data, many cases									
		Period, months: 4-1/3 5-1/18 6-1/15 7 8-3/11 9-1/10 34-1/8							
Wolf sunspot numbers	∨ 20	First half	6	15	17	20	22	20	17
		Second half	12	12	22	19	37	34	23
		Mean	9	14	19	19	29	27	20
	∧ 20	First half	8	7	16	15	20	31	20
		Second half	6	16	11	15	17	20	15
		Mean	7	11	13	15	18	25	17
	Ratio means		1.3	1.3	1.5	1.3	1.6	1.1	1.2
	B. Mean precipitation, Natural Bridge, Ariz., data, many cases								
			Period, months: 4-1/3 5-1/18 6-1/15 7 8-3/11 9-1/10 34-1/8						
	Wolf sunspot numbers	∨ 20	First half	19	18	35	27	43	53
Second half			29	19	40	42	43	59	
Mean			24	19	37	34	43	56	
∧ 20		First half	15	16	23	23	26	42	} 13
		Second half	13	18	26	32	26	33	
		Mean	14	17	25	27	26	37	
Ratio means		1.7	1.1	1.5	1.2	1.7	1.4	1.7	

modifications and improvements in the procedure, which I will not here relate, but which, as will appear, have given still better results in forecasting for my latest work.

Lest readers may suppose that nothing is a true veritable forecast or backcast which deals with time included in the 1,000-month background, I need only remind them that every month forecasted or backcasted depends on the combined influence of 1,000 months of records. In any one year there are but 12 months. Hence the 12 monthly records of that year can have little more than 1 percent influence in dictating the form and amplitude of the predicted curve for that year.

To speak plainly, every year's curve that I am about to show is a real prediction, whether within or before or after the interval of about 1,000 months included in its basis.

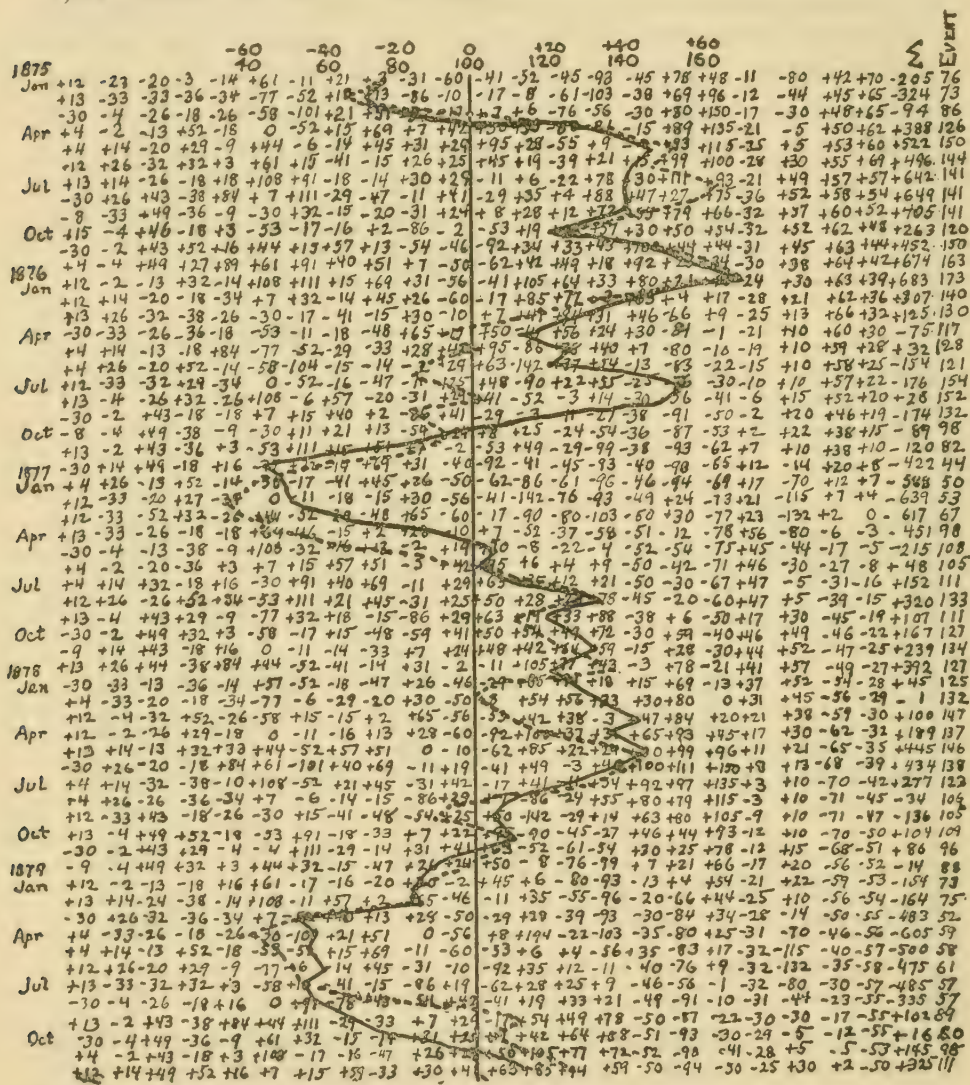


FIG. 7.—Facsimile of computation of St. Louis precipitation, 1875-1879, compared with the observed precipitation as percentage of normal. Data from monthly mean precipitation smoothed by 5-month running means. Dotted curve from summation of 22 regular periodicities, determined as averages over the 86-year epoch, 1854-1939. Full curve, the event.

First of all I show figures 7, 8, and 9 taken from Smithsonian Publ. No. 4211, prepared in 1954 to test the method for the precipitation in St. Louis and Peoria and temperature in St. Louis. A considerable part of these curves give correlation coefficients between

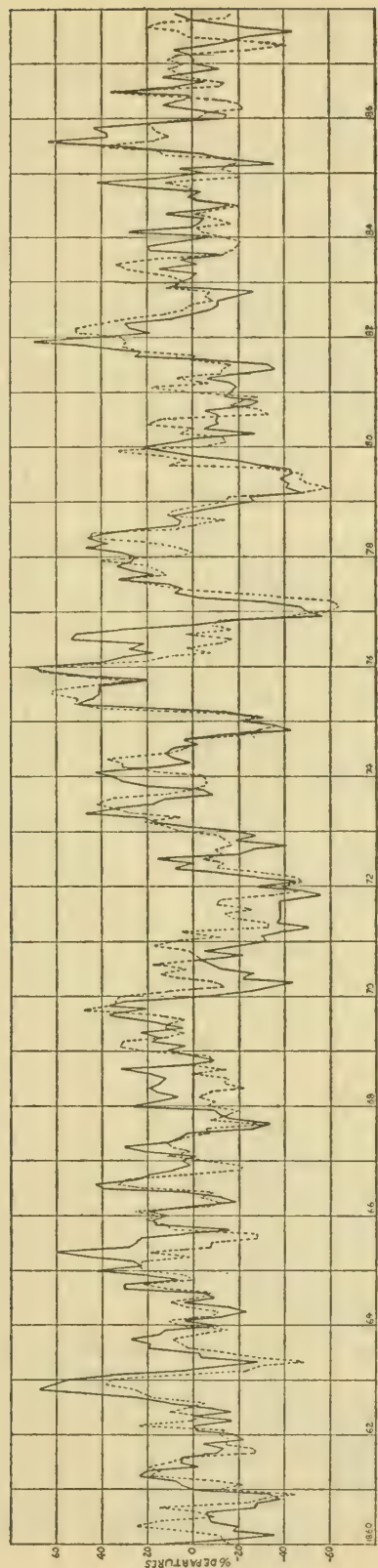


FIG. 8.—Synthesis of computations, 1860-1887, of St. Louis precipitation compared to the event. Dotted curve, computed; full curve, the event. All from 5-month smoothed running means.

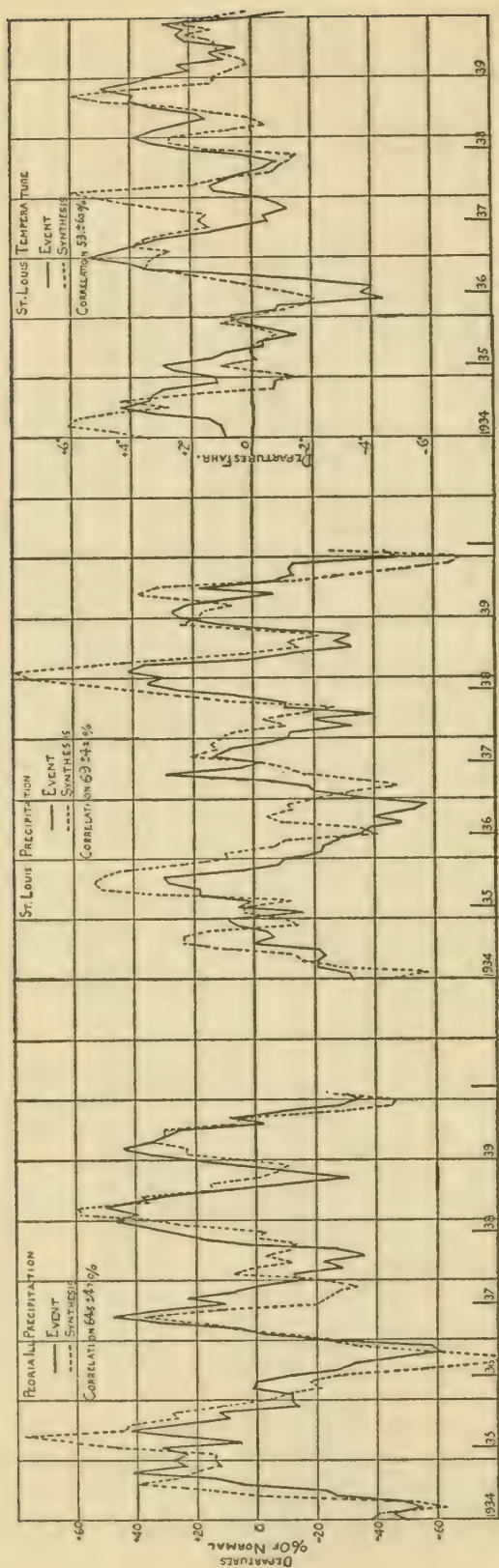


FIG. 9.—Three 6-year predictions 40 years in advance. Precipitation (Peoria and St. Louis) and temperature (St. Louis) computations 1934-1939 compared to the events. Precipitation, percentages of normal; temperature, departures from normal. Dotted curves, computed; full curves, events. All from 5-month smoothed running means.

prediction and event ranging above 80 percent. The results shown in figure 9 for 6-year intervals 40 years from their mean basis, show correlation coefficients from 50 to 70 percent. I repeat the little figure representing St. Louis temperature more distinctly in figure 10.

Although I have stated coefficients of correlation, the method of correlations is not a fair test of the usefulness of the forecast. For when a curve is delineated from the average conditions of 1,000 months at a distance of 40 years from its average source, one cannot fairly expect that the phase of the observed event will never be affected by unusual or accidental displacements due to temporary

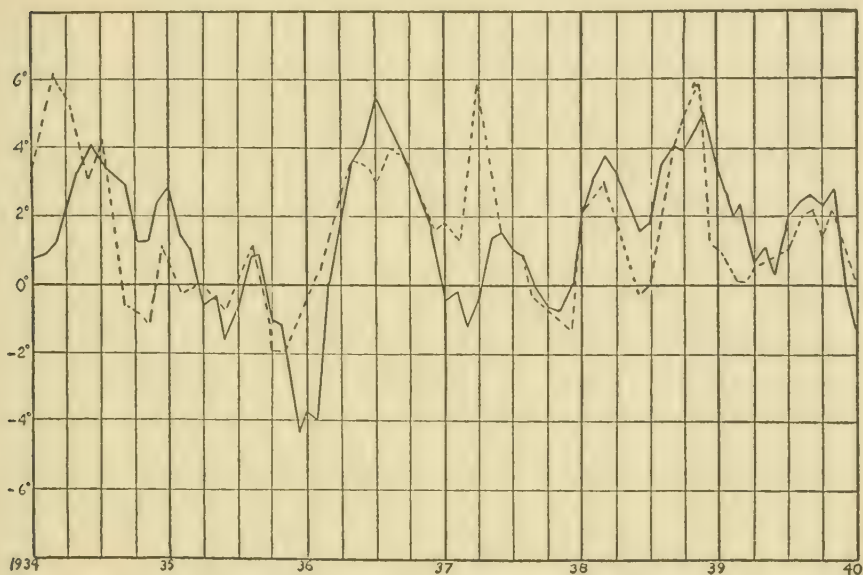


FIG. 10.—Enlargement of temperature forecast for St. Louis shown in figure 9.

causes. Moreover 3- or 5-month smoothing may displace maxima by one or two months. When such displacements of even only one month occur, the curves of prediction and event may often separate widely in ordinates, though to the eye it is apparent that they relate to the same features. In such cases the correlation coefficient is unjustly greatly diminished.

I now show in figure 11 the prediction and event for Washington, D. C., and Spokane precipitation made in 1958 from records centering in 1898 and 1915 respectively, and compared with the observations from 1950 to 1956 available to me at the time. Certain improvements introduced after the Washington work was done helped to make the fit with observation better for Spokane than for any city I have thus

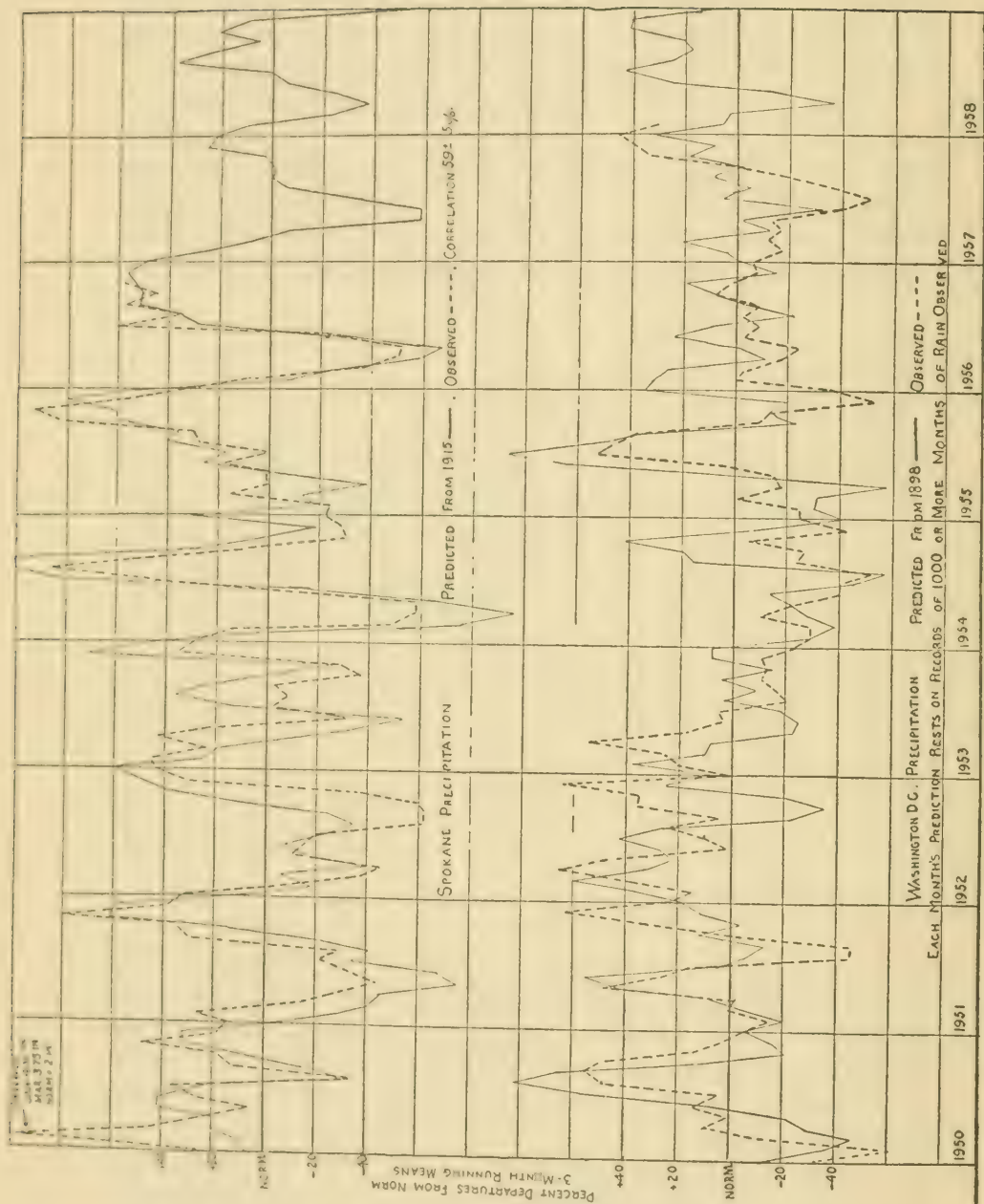


Fig. 11.—Washington, D. C., and Spokane precipitation, 1950 to 1958, forecasted (full curves) and observed (dotted curves), from 3-month running means.

far worked upon. I call attention in figure 11 to very abnormal precipitation in January and March 1950 at Spokane.

6. *The future of the method.*

In 1955 the Association for Applied Solar Energy requested me to test the method on precipitation at the station Natural Bridge near Flagstaff, Ariz. I did so, and the result appears as figure 5 of the paper in the *Journal of Solar Energy and Engineering* above cited. It seemed to the Association of such value that an arrangement was made with Prof. Charles Wexell of Arizona State College to have electronic computations made of precipitation at 30 stations well distributed over the United States. Prof. Wexell's son, Johnathan, cleverly programmed the electronic computer, and has prepared the 220 tables required for each of the 30 stations. Already I have made forecasts for several of the 30 cities with the aid of my secretary, Mrs. Windom, and of Mrs. James Hill, a rapid worker assigned to me by Secretary Carmichael of the Smithsonian Institution. We hope to complete this large program in the coming winter. I propose to publish three maps of the United States for each year, 1959-1967, about April 1959, to delineate the regions of equal departure from normal precipitation in the United States, so far as they can be indicated by these 30 forecasts. A thorough study would require perhaps two or three times as many stations. If this preliminary essay appears useful as time passes, doubtless such a thorough expansion of the work will come.

In the *Bulletin of the American Meteorological Society*, vol. 39, No. 6, June 1958, p. 296, we read: "The petroleum industry estimates that a modest improvement in long-range temperature forecasts would be worth one hundred million dollars a year through more economical operations."

I wrote to Dr. Waterman, the head of the National Research Foundation, that I am sure this can be done, and that with suitable financial aid for electronic computations and other assistance, I believe I could undertake to supply it in 1959, as soon as my present task is over. I would undertake 10-year temperature forecasts for any selected 10 cities in the United States or abroad where about 1,000 consecutive monthly records of mean temperature are available.

Dr. Carmichael, Secretary of the Smithsonian Institution, has allotted funds for a 10-year temperature forecast for 10 cities, which I hope to complete during 1959 as a Smithsonian project.

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BIRDS OF THE PLEISTOCENE IN
NORTH AMERICA

By
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(PUBLICATION 4353)

CITY OF WASHINGTON
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BIRDS OF THE PLEISTOCENE IN NORTH AMERICA¹

By ALEXANDER WETMORE

Research Associate, Smithsonian Institution

Definite formal knowledge of fossil birds in North America began with the studies of Othniel Charles Marsh of Yale University who exhibited bones of seven species before a meeting of the Academy of Natural Sciences in Philadelphia on January 11, 1870, and published descriptions of these and two others in the *American Journal of Science* in March of that same year. In an earlier account Emmons (1857, p. 148) had named a fossil *Palaeonornis struthionoides* that he thought was avian, comparing it to an ostrich. But it is highly doubtful from his account that it was a bird, and since his specimen has been lost it cannot be checked. The first list of fossil birds, published by Elliott Coues in October 1872 as an appendix to his *Key to North American Birds*, included 29 species, all but one described by Marsh. Additions, for a long period, came slowly, mainly through the studies of Marsh, Cope, and Shufeldt, so that the list printed 40 years later in 1910 in the third edition of the *Official Check-list of North American Birds of the American Ornithologists' Union* included only 72 fossil species.

In the years that followed, discoveries of rich deposits directed the attention of those exploring fossil beds more and more to the recovery of smaller animal bones, with increasing impetus to work in the avian field, so that the latest list in 1956 included 449 recognized kinds. The number known increases steadily, the total at present (as of November 1, 1958) being 473 species.

The varied assembly represented gives a fascinating, if fragmentary, view of North America's ancient birdlife—great, toothed divers in the ancient seas of the Cretaceous period; a cursorial

¹ Presented November 12, 1958, at the University of Michigan, as the Ermine Cowles Case Memorial Lecture, under the sponsorship of the Museum of Paleontology, the Geology Department, and the University of Michigan Chapter of the Society of Sigma Xi.

American vulture in company with flightless running birds of ostrich size on open lands of the Eocene; a strange family (with four known species) allied to the South American cariamas, and the first known song bird, in the Oligocene; a tiny parakeet, and an assembly of hawks of much variety in form, in the Miocene; and flightless auks and dwarf cranes in the Pliocene; to indicate only a few of the birds whose remains have been discovered in the vast reach of time encompassed in the Tertiary. Finally there are the deposits of the Pleistocene where remains of species now extinct mingle with those of birds still living. Let imagination clothe these bones with flesh and feathers, and we have a marvelous view of the interesting form presented by these birds of the past, even though this must remain in monochrome since the fossil record does not present the varied colors that must have been found in the feathers of life.

It has seemed appropriate to review in some detail the birds known from the Pleistocene, since among these we have the immediate background of the series we know in life today. In this discussion the terms Pleistocene and Ice Age are treated as synonymous.

THE PALEONTOLOGICAL RECORD

General.—In brief outline, climate in North America during the latter half of the Tertiary, except for differences in humidity, is reported as more uniform than that known from direct human experience in historic years. Plants and animals whose modern kinds are of subtropical habit ranged far north in Miocene times until finally, following the Pliocene, there came the southward movement of glacial ice that marked the beginning of the Pleistocene. While slow change in climatic condition may have enabled some species to adapt to the increasing cold, the advance of the ice front steadily covered more and more of the northern range to displace even the adaptable kinds farther and farther to the south. Geologists recognize four periods during the million years of time usually assigned to the Pleistocene during which the ice front advanced southward, with intervening periods of interglacial time, each of greater length than the preceding glacial tenure, when retreat of the ice left the northern land and water areas open and habitable again. Flint (1957, p. 301) estimates that the termination of the last of the glacial periods came within the past 30,000 years.

The present avifauna of North America, north of the Mexican border (but including the peninsula of Baja California), according to the latest check-list of the American Ornithologists' Union (1957)

includes a total of 796 species. Among these there are 87 kinds reported from stray individuals that have wandered into the area accidentally from other regions, and 12 more, such as the ring-necked pheasant, starling, and house sparrow, that have been established through introduction by man within the historical period. If the sum of 99 in these two categories is subtracted from the total, there remain 697 species that may be considered to constitute the normal present-day avian population of that part of the North American Continent under discussion. Remains of 190 of these, or nearly two-sevenths of the entire list, have been found to date in deposits of Pleistocene age. Seven more which may be included have come from this same period in Cuba and Nuevo León, making a total of 197. To complete the census there must be mentioned also the wood rail (*Aramides cajanea*) found from southern Tamaulipas south to northern Argentina and Uruguay, whose bones have been identified in Pleistocene beds in west-central Florida. There are 83 extinct species in addition that have been described from Pleistocene deposits, making a total of 281 kinds now known from this period.

Early collectors of vertebrate fossils found such quantities of the remains of large, impressive animals—fishes, reptiles, amphibians, elephants, ground sloths—that small bones like those of birds, if any were present, were passed over as unimportant. The actual record of our Pleistocene avifauna in any detail began about 1870 when Cope and Marsh described bones of turkeys found in Monmouth County, central New Jersey. The first important find of a quantity of remains of Pleistocene birds was at Fossil Lake in the desert region of Lake County, Oreg. The deposits here, brought to attention by Governor Whiteaker, in 1876, and explored in 1877 by Thomas Condon, yielded “eighty bird bones which were unusually perfect and in a fine state of preservation.” More were collected the same year by Charles H. Sternberg, for Prof. E. D. Cope, who visited the area personally in 1879. Condon, whose specimens are now in the paleontological collections of the University of Oregon, described the site as a “depression four to five miles across, with some grass and tules in its lowest portions, and in the middle a small pond or lake.” The fossils often were exposed by wind blowing away the surface sand and dust.

Cope (1878, pp. 386-389) identified 10 species of birds in the first collections, describing three as extinct; and then later, when he became occupied with other studies, placed the main series in the hands of R. W. Shufeldt. Shufeldt's detailed report (1892) covered 50 species of birds, and in all he described 14 from Fossil Lake as new to

science. Others worked the deposit from time to time, with further publications as a result. Finally, Hildegarde Howard (1946) assembled all the material available in the seven known collections, in which she was able to identify 2,500 bones to the family represented. Her final tabulation covered 60 identified species, of which 15 are known only in fossil state. The majority are aquatic, as would be expected from the nature of the deposit, the remains of grebes, cormorants, geese, ducks, and coots predominating. An extinct flamingo (*Phoenicopterus copei*) is an unusual member of this avifauna in view of the present-day distribution of its group. Three of the five recorded species of grouse are extinct, and a large cormorant (*Phalacrocorax macropus*), a swan (*Cygnus paloregonus*), two extinct geese, a duck, and two gulls are other interesting elements in this ancient assembly.

Conditions may not have been suitable for the preservation of skeletons of smaller animals, though possibly small bones may have been overlooked through the older methods of collecting under which most of the materials were obtained. Only 15 bones of passeriform birds have been identified, including one specimen each of the living raven and Brewer's blackbird. Small mammal remains are scanty also, since Elftmann (1931) lists only a meadow mouse and a pocket gopher. The site, now usually completely dry, is in a circular depression that in Pleistocene time was joined with nearby Christmas and Silver Lakes to form one body of water. The fossil avifauna as a whole is indicative of a plains environment and is the first comprehensive one of its period known in the western part of North America. At present the deposit is interpreted as late Pleistocene in age.

Since the earlier years of the present century there have been reports of a "duck sickness" that periodically has killed large numbers of aquatic birds, principally in the Great Basin area of the West, and sporadically elsewhere. Because of the importance of this group as game, the main publicity has been given to the hundreds of thousands of wild ducks that have died, but practically any species of bird that visits shallow waters in the drier period of late summer and early fall may be affected. It is proved now that the mortality is due to a toxin, generated under certain conditions by a bacterium, *Clostridium botulinum*, type C, obtained by the unsuspecting birds that feed in places where the lethal element is produced. When I remember the long rows of bird bodies that I have seen rotting and drying around pools and channels at the mouths of streams draining into Great Salt Lake, I have wondered whether some similar condition in Pleistocene times may have led to such accumulations of bones of birds as that

found at Fossil Lake. Certainly the similarity in the kinds of birds affected is suggestive.

Following the early explorations in Oregon there came occasional reports of cave and other deposits from which a few bones of birds were obtained, but these and all others have been completely overshadowed by the collections made in the asphalt pits of Rancho La Brea in the present city limits of Los Angeles, Calif. These deposits were recorded in the diary of Gaspar de Portola under date of August 3, 1769, with the observation that mammals and birds driven to seek water around the pitch pools in this area often became caught in the viscous tar where they were held until they died. The first scientific record that the asphalt pools had served as a trap of this kind for thousands of years came in a letter from William Denton, published in the Proceedings of the Boston Society of Natural History in January 1876. During a visit to Major Hancock's Brea Ranch, where the asphaltum was dug to be marketed for paving material, Denton obtained a number of bones of fossil mammals, and one of a bird, recorded as an "albatross" (whose actual identity remains today unknown). In spite of this early reference it was not until 1905 that the potential scientific importance of these beds was recognized by W. W. Orcutt. Some fragmentary mammal bones collected by Orcutt and Frank M. Anderson were sent to John C. Merriam at the University of California, who realized at once the possibilities. Collections instigated by Merriam were made by representatives of the University at intervals from 1906 to 1913, when excavation privileges were granted to Los Angeles County, and the work was continued by the institution now known as the Los Angeles County Museum. The vast collections obtained have included over 100,000 bones of birds from which 92 species, 15 of them no longer living, have been identified, mainly through the careful studies of Loye Holmes Miller, Hildegard Howard, and Alden H. Miller.

The locality is on the coastal plain in an area that seems to have been mainly open country. Analysis of the complete fauna, including the mammals, and of the plant remains indicates a Pleistocene climate of an interior type, with rainfall moderate. Petroleum in quantity came to the surface through scattered vents, to form pools in small depressions. Exposure to the air caused dissipation of volatile elements, leaving heavier components that developed crusts covering viscous materials of increasing density. As similar conditions have continued at Rancho La Brea until the present day, this has aided in interpretation of the story of the past. The surface often was so

covered with dust that its viscous nature was concealed. In places there were scattered pools of water, with herbage growing about them. Unwary creatures, large and small, became caught in the tar, when grazing, when in search of water, or when merely crossing open areas. The immobility of these, and their struggles when alive, attracted predators—saber-toothed tigers, wolves, eagles and other hawks—which in turn were caught. And the bodies of predator and prey called the carrion-eaters, both bird and mammal, and these also left their bodies in the tar. The whole formed an automatic trap, continuous and deadly in operation, that has persisted for millennia. As the bodies sank gradually into the asphalt, flesh disappeared, and slowly the porous parts of the bones became impregnated with tar, with the result that preservation has been complete and perfect. Slow movements of the mass of asphalt have scattered the parts of the bodies so that completely associated skeletons are not found, but the separate elements often were encountered in local concentrations in great abundance.

Two other asphalt deposits have added to our information of the bird life of California during the period of the Pleistocene. John C. Merriam and Chester Stock in 1921 gave the first formal notice of one near McKittrick in Kern County, including records of birds that had been identified by Loye Miller. The deposits here were in a fairly level, open valley, where there is indication of the former existence of extensive ponds or lakes of shallow water, with the usual border of marshy grasslands and mud flats. There are more ducks, cranes, herons, shorebirds, and other aquatic species here, and fewer of the great vultures, than at Rancho La Brea. Ten of the 64 species of birds recorded are forms now extinct, two of them—a falcon and a goose—not found at the other site. The avifauna as a whole is an assemblage to be found around fresh water, with general resemblance to that of Fossil Lake, Oreg.

The third of these major pitch deposits, near Carpinteria in Santa Barbara County, came to attention in 1927. The site is at the coast and seems to have been in a partly forested area, in a region of greater humidity than the other two. The deposit is marked especially by the detailed preservation of delicate plant materials, including flower parts and epidermal layers of leaves that are seldom found in fossils. Forty-eight species of birds are reported, of which ten are extinct.

In the eastern half of North America the most important collections of Pleistocene bird remains to date have come from Florida in

locations including caves, stream beds, springs, and accumulations in sand and other deposits. In 1931 I published a detailed account of the Pleistocene birds from eight localities scattered through the State that included 63 species, of which three were extinct. The most striking of these was the great condor *Teratornis* hitherto known only from California. But also of interest are the fossil stork *Ciconia maltha*, here recorded for the first time outside California, and the living wood rail *Aramides cajanea*, already mentioned as today confined to tropical America. In recent years Pierce Brodkorb at the University of Florida has added steadily to our information until at present the total list of Pleistocene birds from the State includes 97 species, of which 12 are no longer living.

In addition to these major areas there have been finds of Pleistocene bones of birds at many scattered localities, including one recently in southern Ontario, the first for Canada. The main area now of greatest promise is in the Great Plains in southwestern Kansas and adjacent Oklahoma where work is going forward under the direction of Claude W. Hibbard of the University of Michigan. Study of the considerable amount of bird material, much of it procured by careful sifting and washing of unconsolidated earth, is only in an early stage, so that the 14 species of birds recorded to date are merely an indication of the considerable number still to come.

The probability of preservation of skeletal remains of birds, in spite of their abundance as individuals, is relatively small, since skull and sternum are fragile, and the longer limb bones, while firm in texture, usually are hollow so that the shafts crush easily. The result is that fossil remains are rare. In scanning the fossil list it is evident that the majority of the recorded species are medium to large in body, implying that larger size, coupled with stronger structure, is definitely a criterion in preservation, as well as an aid to the collector in finding fossil remains. It is rare that parts of a skeleton are found associated, and exceptional when a complete fossil skeleton is encountered. The paleornithologist early learns to find enthusiasm in fragments of bone that to the uninitiated may appear without character or attraction.

It should be noted that in a few instances a few fossil materials have been identified in terms of distribution of modern species without regard to whether there may exist osteological differences. Thus, in compiling fossil lists we find records of eastern and western meadowlarks, and of three species of flickers, where so far as I have been able to ascertain the skeleton permits certain identification only

to the genus. In preparing the statistics that I give in the present paper I have treated each of these groups as one.

Among the 281 species of birds now known from the Pleistocene the family of ducks and geese, with 38 kinds recorded, has the largest representation. Eight of these are extinct. Many of the deposits in which fossil bird remains are found were laid down in lakes, ponds, and marshes, or in pitch deposits where water on the surface may have been an attraction, so that the abundance of this group is a natural outcome in view of the size of these birds, and of the gregarious tendencies that draw them together where water and food are present.

The 42 kinds of the 4 families of falconiform birds, the vultures, hawks, falcons, and the osprey, may be explained in part by the attraction of some of them to dead animal bodies, fresh or decomposed, in the tar pits, and to the habit of many of nesting or roosting in caverns, in addition to the usual circumstances in which their bones have been preserved through their durability. The extinct species number 19, of which 6 are of the two families of American vultures (Cathartidae and Teratornithidae). Birds of this order were evidently more abundant in Pleistocene times than at present, as the modern list of the four families concerned within our limits includes only 37 species.

Pleistocene grouse, quail, and turkeys number 18, the rails 13, the shorebirds—plover, sandpipers, avocets, and phalaropes—19, the two families of owls 16. The smaller perching birds have their best representation among the species of more robust form, the crows and jays numbering 12, the blackbirds 9, and the finches and sparrows 20.

Ciconiiformes.—Today two storks are known from North and Middle America from the Isthmus of Panamá northward, the large-headed jabiru (*Jabiru mycteria*), with straight heavy bill, and the wood ibis (*Mycteria americana*), smaller in size, marked by a bill that curves downward at the tip, like that found in the related family of true ibises (Threskiornithidae). Possibly the jabiru had a South American tropical range, during the Pleistocene, since it has not been reported to date from North American fossil deposits. Instead we find a quite different species, *Ciconia maltha*, which is so abundantly preserved at Rancho La Brea that the complete skeleton is known. This bird was about $4\frac{1}{2}$ feet tall, with slender legs, in which the tibiotarsus was by far the longest element. The bill is long and slender, and the wing also long. Because of the slender bill this bird is currently listed in the genus *Ciconia*, which contains the true storks

of the Old World. It may be noted, however, that the slightly concave curvature of the upper mandible is suggestive more of the much larger-billed jabiru, a species with heavier frame throughout, than it is of the true storks (genus *Ciconia*), in which the slightly less attenuate bill is moderately convex in dorsal outline. It is probable that the fossil will be assigned to a separate genus when a fully adequate series of skeletons of modern storks is available for study. *Ciconia maltha* was widely distributed, as it has been recorded from the three asphalt deposits, from another fossil bed in San Bernardino County, Calif., and from Idaho, Florida, and Cuba. It has been identified also from the Hagerman Lake beds of supposed Upper Pliocene age on Snake River, Idaho.

The second fossil stork, named *Mycteria wetmorei* by Hildegard Howard, is known from parts of the upper mandible, leg, and wing from Rancho La Brea. The species resembles the living wood ibis found from the southern United States south to northern Argentina, but was at least one-third larger, perhaps of even greater size, so that in bulk it may have been nearly equal to the jabiru.

Two species of flamingo add a somewhat exotic note, since here in the United States usually we think of birds of this group as subtropical, as that is the present range of the American flamingo (*Phoenicopterus ruber*) of our check-list. The distribution of this species may be due more to choice of habitat than to climatic conditions, since another living species ranges south into Patagonia, and two others are found around Temperate Zone lakes high in the Andes. The best known of the fossil species, *Phoenicopterus copei*, is from the Pleistocene of Fossil Lake, where a number of its bones have been collected. It seems to have been slightly larger than the American flamingo, with stronger, heavier legs. A leg bone of an immature bird, apparently not fully grown, found in late Pleistocene deposits at Manix Lake, east of Barstow, Calif., probably represents *P. copei*. A second species, *Phoenicopterus minutus*, from Manix Lake, was decidedly smaller, being about three-fourths the size of the American flamingo. It is the dwarf of the genus as at present known.

Anseriformes.—At Fossil Lake, Oreg., the thousand or more bones of the Anatidae, including 25 different kinds, outnumbered those of any other group. The most interesting species is a swan, *Cygnus paloregonus*, as large in bulk as the great trumpeter swan, but with shorter legs and longer toes. In the two living North American swans the trachea, or wind pipe, as it passes from the neck into the body, makes a long loop within the bony frame of the sternum and then

divides and continues to the lungs. The fossil species belongs to another group, which includes the living black-necked swan of South America, in which the trachea has the normal straight form.

The most abundant fossil of this order in marine beds of Pleistocene age near the coast of southern California is a flightless, diving species, *Chendytes lawi*, formed like a scoter, but in body size approaching a goose. The wings were small, and the humerus and scapula were degenerate, suggesting a condition like that current in the larger flightless rails. It is indicated that the wing actually lacked function related to movement. The legs on the contrary were large and strong, and the pelvis heavy, proof of the diving habit. A second species, *Chendytes milleri*, from earlier Pleistocene beds on San Nicolas Island, Calif., somewhat less in size, had the humerus small but more normal in form. It is supposed that this second bird, while flightless, represents a stage less specialized in this direction than its companion species.

In 1924, in study of a small collection from the Benson local fauna of Blancan age in the Upper Pliocene of Arizona, I named a tiny goose, like a mallard duck in size, that later was placed by Ross in a distinct genus, so that it is known now as *Anabernicula minuscula*. Apparently this pygmy goose was common and widely distributed throughout the Pleistocene, as it has been recorded at Fossil Lake, Oreg., in asphalt beds at Rancho La Brea and McKittrick, Calif., and in the earthen floor of Smith Creek Cave in eastern Nevada. In some characters of the humerus *Anabernicula* is unlike any of our living groups, as it resembles certain ducks, though otherwise the skeleton so far as this is known suggests a goose. It is probable that the genus will be placed in a distinct subfamily when it is better known.

Falconiformes.—The great order of hawklike predators and scavengers, as stated, is abundantly preserved in Pleistocene deposits. The group is especially represented at Rancho La Brea, where falconiform remains constitute considerably more than half of the more than 100,000 bird zones collected.

Two extinct falcons and a caracara of the family Falconidae are fairly close to kinds still living. The 10 defunct species of the hawk family (Accipitridae) are more peculiar, since they include two, *Neogyps errans* and *Neophrontops americanus*, that have affiliation with the subfamily Aegypiinae, the Old World vultures, whose living forms are restricted to Eurasia and Africa. While in structure these are true hawks, in habit they are more the counterpart of the scavenger American vultures (Cathartidae). *Neophrontops* is suggestive

of the modern Egyptian vulture (*Neophron percnopterus*), a species that in spite of its common name is widely known in southern Europe, southern Asia, and throughout much of Africa. The genus *Neophrontops* has a long history in the New World, as one species has been described from the Middle Miocene of Nebraska and another from the lower Pliocene of South Dakota. The Pleistocene bird, known from California and from a cave in Nuevo León, about the size of a turkey vulture but more robust in form, lived in California until postglacial time, as its bones have been found at Rancho La Brea in pits associated with ancient man.

The companion, *Neogyps errans*, of heavier, more stocky build, had an equivalent Pleistocene distribution in California and Nuevo León and has been found as well in cave deposits in Nevada. Three additional fossil species of Aegypiinae have been described from the Miocene and Pliocene of New Mexico, Nebraska, and South Dakota.

Among the eaglelike birds from the asphalt pits, one of the outstanding species is Daggett's eagle (*Wetmoregyps daggetti*), with the body size of a golden eagle, but mounted on long, slender legs. The general form is that of the modern great black hawk (*Hypomorphnus urubitinga*) that lives a sluggish life in open woodlands and forest borders in tropical America, feeding on frogs, snakes, and similar rather easily procured food. The fossil species is assumed to have had somewhat equivalent habits.

While those just mentioned are of interest, the greatest attraction to me in the falconiform group centers in the condors and related vultures. The living black vulture (*Coragyps atratus*) is a resident of tropical and warm temperate areas in continental America from southern Arizona, southern Illinois, and Maryland south to northern Patagonia and southern Chile. To date, its bones have been found at two localities in the Pleistocene of Florida. There was a related species, *Coragyps occidentalis*, widely distributed in Pleistocene times, that differed from the living bird in larger head, heavier body, and shorter, heavier legs. The living species is gregarious, found often in groups not only at night roosts but also during the day as well, when it gathers in companies to feed at carrion. The abundance of remains of the extinct species in a few localities indicates similar habits. It is recorded from Pleistocene sites in California, Nuevo León, and Florida, and in Quaternary deposits that may be Pleistocene in Nevada and New Mexico. Recently it has been found on the Oregon side of the Columbia River near The Dalles at Indian campsites with an age of a little less than 8,000 years as established by

carbon-14 dating. No reason for its extinction is evident, particularly since bones of the turkey vulture (*Cathartes aura*), a species still abundant, have been found associated with it at localities in California.

Condor remains are widely spread in localities in California, Nuevo León, New Mexico, and Florida and are known also from prehistoric cave deposits in Nevada and Texas, a former range for these great birds across the entire southern part of our country. Bones of condors from the Pleistocene indicate somewhat greater size for the largest as compared with the largest of modern individuals, though in the series there is definite overlap in which a good many might belong to either the modern or the extinct group. Difference is most evident in the skull, but even here the distinction is not clear-cut. The Pleistocene bird at present is called *Gymnogyps amplus*, as distinguished from the modern California condor, *Gymnogyps californianus*. Perhaps the differences between the two groups might be presented appropriately as subspecific, in terms of what George Gaylord Simpson has called a chronocline, where the relationship is one found in geologic time, instead of the modern situation in which subspecies have separation in geographic space.

The most exciting of the great condors is the extinct *Teratornis merriami*, found first in the asphalt pits in California. Later I identified it from the Pleistocene of west-central Florida, and recently Loye Miller has reported it from Cueva San Josecito in Nuevo León. *Teratornis* is especially abundant at Rancho La Brea, where remains representing more than 100 individuals have been recovered. The bird was vulturelike in form but differed from modern condors in heavier skull, compressed, arched beak, in side view almost like that of an eagle, and in a sternum that was greatly broadened at the anterior end so that it was wider than long. The wing elements were long, with heavy muscle attachments on the humerus, and those of less development on the outer part of the wing. The segments of the lower limb, on the contrary, while somewhat heavier, were about the same in length as those of Pleistocene California condors, except for the tarsometatarsus which was a little longer. It is estimated that *Teratornis* may have had a weight of 40 to 50 pounds compared to a maximum of 23 pounds for the living California condor. The wing spread in a composite mounted skeleton in the Los Angeles County Museum is 7 feet 3½ inches. When the estimated length of the flight feathers is added, the span of wings in life may have been at least 12 feet, or a little over 2 feet more than that of the largest condors. The structure of the legs is such that the bird may have taken flight by springing

into the air after a few running steps, like a black vulture, rather than through a longer run to gain momentum, like a condor. The type of wing musculature indicates flapping flight, and also ability at soaring in supporting air currents, here again resembling the black vulture.

Teratornis merriami was huge compared to living species but was completely eclipsed by *Teratornis incredibilis*, described by Hildegarde Howard from a single wrist bone found in a cave in Nevada. In form this closely resembles *merriami* but is nearly twice as large as the corresponding element in that species. The indication is that it was the largest flying bird yet known. Truly there were giants among the birds in Pleistocene days.

In summary, the hawklike birds have varied more from modern types than the Anseriformes, since 21 of the 42 species are extinct. The American vulture group was more diversified in Pleistocene times in North America than now, since 8 species of two families are known, contrasted with 4 of a single family recorded in historic times. The hawks with 25 species in the Pleistocene and 26 found today, and the falcons with 9 fossil species and 7 in modern times, seem to have maintained an equivalent ratio of abundance.

Galliformes.—The 21 species of fowl-like birds of the North American Pleistocene include 10 that are extinct. Among these, those of the greatest interest are the turkeys. The California turkey (*Parapavo californicus*) apparently was a common bird in the coastal area of southern California, as bones of about 700 individuals, including numerous poults, were recovered at Rancho La Brea. The species was numerous also at Carpinteria. The adult was smaller than the modern wild turkey and in characters of the skeleton seems intermediate between that group and the tropical ocellated turkey (*Agriocharis ocellata*) of the Yucatán Peninsula and adjacent British Honduras and Petén. There is record of *Parapavo* also from the Upper Pliocene of northwestern Texas. At Rancho La Brea it lived into early Recent time, as its bones have been found associated with remains of man in one of the excavations.

Other extinct turkeys include one described from Florida from the tarsometatarsal bone of a male in which the usual single spur was modified to a heavier, 3-pointed weapon. Another from a cave in Nuevo León had exceptionally heavy feet. The modern wild turkey has been recorded frequently in fossil form, including the Rexroad formation of the Upper Pliocene in Meade County, Kans., and 16 localities of Pleistocene age in New Mexico, Illinois, Indiana, Arkansas, Tennessee, Pennsylvania, and Florida, a range that covers most of the modern distribution of these birds north of México.

Gruiformes.—The whooping crane (*Grus americana*), now reduced to about 40 living individuals, has been found fossil at Rancho La Brea in California, though in modern times it has not been known in the United States west of Wyoming, Colorado, and New Mexico. Elsewhere, fossil records of it come from Florida. The sandhill crane has been reported fossil from California to Florida, all within its modern range. The limpkin, living now within the United States only from southeastern Georgia south through Florida, is known from three Pleistocene localities in the latter State.

In the family of rails 13 species have been reported from fossil beds, 4 of them extinct. Remains of coots include the American coot (*Fulica americana*) in California, Nevada, Nuevo León, Texas, and Florida, so that it had a range continent-wide, then as now. A relative, *Fulica minor*, is reported at Fossil Lake, Oreg., and in Florida. One extinct rail, *Laterallus guti* (Brodkorb, 1952, p. 80), is representative of the living black rail, while another, *Porzana auffenbergi* (Brodkorb, 1954, p. 103), a species larger than the living sora, is one whose line appears to have become extinct. Both come from Florida.

Passeriformes.—There are more birds of the order Passeriformes today, worldwide, both in species and individuals, than are found in all the other orders combined, but the small size of all but a few and the fragility of their bones thus far have restricted our knowledge of their fossil history. It is only recently that there has been systematic search for remains of the smaller vertebrates in general, and much of the passeriform bird material recovered still awaits identification. It is interesting to record, however, that 58 species are now known from the Pleistocene, 8 of them extinct. The considerable collections made by C. W. Hibbard and his students in Kansas and Oklahoma, and other materials collected by Pierce Brodkorb in Florida are certain to expand these numbers considerably.

The crow-jay family (Corvidae) is the best represented, with 11 fossil kinds. These include two species of ravens, three of crows, two of magpies, and four of jays, all living kinds. The group seems to have had diversity in the Pleistocene more or less equivalent to what is known today. The one extinct jaylike species, *Protocitta dixi*, from Florida, is related to forms living in México, so that it brings an additional element into our northern avifauna.

The blackbird and grackle family (Icteridae) has 9 Pleistocene species, of which 4 are extinct. The living kinds include meadow-larks, reported from California and Florida, red-winged and Brewer's blackbirds, and purple and boat-tailed grackles. One of the extinct

species, *Euphagus magnirostris*, from Rancho La Brea, seems to have resembled the Brewer's blackbird, except for heavier beak. Another, *Pyelorchamphus molothroides*, related to the cowbirds, also had a stronger bill. Two other kinds, *Pandanaris convexa* and *P. floridana*, the first from California and the second from Florida, were generalized forms of a blackbird-cowbird type that has become extinct.

Finches and sparrows (family Fringillidae), abundant today, were common also in the Pleistocene, from which 20 forms have been identified. These include black-headed and evening grosbeaks, American goldfinch, pine siskin, red crossbill, lark bunting, two species of towhees, and numerous sparrows. Only one, a towhee, *Pipilo angelensis*, is extinct. This bird, a little larger than living kinds of the genus, was marked by differences in the bill. Other extinct passerines include a swallow, *Tachycineta speleodytes*, somewhat like the tree swallow, and a wren, *Cistothorus brevis*, allied to the short-billed marsh wren, both from Florida.

Extinct birds from West Indian caves and kitchen middens.—To complete this enumeration it is pertinent to notice several extinct species, certainly of Pleistocene history in their evolution, but known only from bones found in caves or in kitchen middens in the West Indies. The cavern deposits are of uncertain age, but they have been estimated to antedate the historic period by 1,500 to 3,000 years, and in some cases may have had much greater antiquity. A huge hawk, *Titanohierax gloveralleni*, from Great Exuma Island in the Bahamas, allied to the living tropical great black hawk (*Hypomorphnus urubitinga*), was of eagle size but with much longer legs. In the same deposits were leg and wing bones of a barn owl, *Tyto pollens*, about as tall as the modern great horned owl, that also was a giant of its kind. I have named a related large species *Tyto ostologa* from caverns in Haiti, and have now bones of a much larger one from a cave in eastern Cuba that I have still to name and describe. These owls lived with a fauna of extinct rodentlike mammals, known only from their bones found in caves. It is undoubtedly the regurgitated food pellets of the great owls that built up a large part of the cavern bone deposits.

A curious rail, *Nesotrochis debooyi*, was found first in prehistoric Indian kitchen middens in the Virgin Islands and later was encountered in cave deposits in Puerto Rico. While the cavern beds have not been dated, the bird remains in them are associated with small ground sloths (*Acratocnus major*, *A. odontrigonus*), indicative of an antiquity extending back toward the Pleistocene. An extinct agouti (*Isolobodon portoricensis*) shared with the rail as a food

source for these Indians, as the bones of the two are found together in the middens. The rail, about the size of a small chicken, seems to have been related to the wood rails of the genus *Aramides*, of wide distribution now in the American Tropics. The extinct species differed in more robust legs and heavier pelvis and, more definitely, in a slender, strongly curved humerus, with the processes for muscular attachment on the proximal end so slightly developed as to indicate that the bird must have been flightless.

Years ago during fieldwork in Puerto Rico, I was told that a bird called the "carrao" was hunted with dogs in early morning when the vegetation was so wet with dew that the feathers of the quarry soon became water-soaked so that it could be caught by hand. In modern times the native name "carrao" is applied to the limpkin, *Aramus guarauna*, a wary species that flies at any alarm, like a heron or an ibis. Since my discovery of the abundant bones of the flightless rail, I have pondered the probability that *Nesotrochis* may have been the "carrao" of earlier days, as its flightless state would have enabled its capture by the method described.

Family representation.—The Pleistocene list to date includes representatives of 56 of the 72 families of birds on the North American list. Most of the known fossil deposits of this age are of fresh-water origin, or are located in interior regions remote from ocean beaches, so that the lack of such marine species as storm petrels, tropicbirds, frigatebirds, and skimmers is not surprising. No kingfishers are known as yet, and jaçanas and trogons are missing. The absence of chachalacas and curassows (family Cracidae) is worthy of note, since five species of this group have been described from deposits of Upper Oligocene, Lower Miocene, and Lower Pliocene age, in South Dakota, Nebraska, and Florida. In modern times the family has been confined to tropical areas from México south to northern Argentina, with a few species ranging into the subtropical zone in the mountains. Only one, the chachalaca, now extends north into extreme southern Texas. Absence of Cracidae in the North American Pleistocene may be attributed to climatic changes that may have forced them south in late Pliocene times. The other families not yet recorded include species in the main of such small size—swifts, hummingbirds, and various groups of Passeriformes—that their fossil remains either have not been found or have not been identified.

DISCUSSION

As already stated, until late Miocene times subtropical conditions prevailed through the greater part of what is now the temperate area

of North America, but by late Pliocene the limit of the subtropics had shifted until it was closely similar to that of the present. The advance of the first ice sheet as it moved the tundra and the colder zone forests southward, drove bird species of warmer habitat preference southward against the unyielding water barrier of the Gulf of Mexico in the east, and against the more resilient resident tropical avian populations of México in the west. The succeeding interglacial period then permitted reversal of this movement as habitable lands opened again toward the north. As these major conditions were repeated four times, according to present understanding of Pleistocene history, it was apparent that ebb and flow in distribution has been the history of the North American avifauna for the past million years.

The method of progression in geographic range following retreat of glacial ice may be understood through examination of recent climatic change in Greenland, Iceland, the Scandinavian Peninsula, and Finland. During the past hundred years weather records show a slow but steady advance of warmer temperatures toward the north, a shift that has accelerated since about 1920. In the southern half of Finland, for example, Merikallio (1951, pp. 487-488) reports that the brambling (*Fringilla montifringilla*), a finch of northern affinity, since 1930 has been largely replaced as a breeding bird by spread of the less hardy chaffinch (*Fringilla coelebs*).

In Iceland, Gudmundsson (1951) informs us that through warmer conditions in the past 50 years, under which glacial ice has retreated and winter pack ice has decreased on the northern coast, seven species of birds have been added to the breeding population, including such diverse forms as the starling, short-eared owl, herring gull, and tufted duck. There has been increase also in migrant kinds and in birds that remain through the winter.

In Greenland, Salomonsen (1951, pp. 483-489) records a far more impressive instance, in which late in January 1937 there was a chance invasion of a flock of Old World thrush, the fieldfare (*Turdus pilaris*), a species that nests in coniferous and birch forests of northern Europe and northwestern Siberia, ranging north to near the limit of trees. In the interior of the Julianehåb District in southwestern Greenland the invaders remained to establish a breeding colony, thus populating a land area quite remote from their previous range.

While some of these birds, e.g., chaffinches and starlings, migrate, in part at least, in fall to return in spring, the hardy fieldfare, though migrant in northern Eurasia, remains resident in southern Greenland.

It seems reasonable to believe that as birds spread into the expand-

ing open areas during the close of Wisconsin time in the Pleistocene, there came movement in and out of these regions that continues in the fall and spring flights of the millions of birds that each year nest in northern areas where they can not remain through the period of winter cold.

The question of the extent of modern migrations is one of interest. Among the multitudes of migrants that come south into Central America, eastern and western species mix in abundance as far as southern Guatemala. Farther south, eastern species predominate, and comparatively few of those that nest between the Rocky Mountains and the Pacific coast reach the isthmus of Panamá.

A possible explanation may be found in the situation outlined above, when the ice front of the last glacial period in the eastern half of North America extended south to Long Island, the Ohio River Valley, and the Missouri River above St. Louis, with consequent displacement of Temperate Zone conditions far southward. In the west where the ice front lay a relatively short distance below the United States-Canadian boundary, with only limited local glaciers in the mountain areas, pressures toward the south would have been far less severe. Eastern species either had to cross the water barrier of the Gulf or to follow the shoreline west and southwest, and so tended to penetrate farther into Central America. Western populations on the other hand had necessity for shifts of less extent.

One of the mass annual movements among modern small birds that has long stirred my imagination is the migration of a small group of vireos of several closely allied kinds. The red-eyed vireo (*Vireo olivaceus*) breeds commonly over a broad area from British Columbia and the eastern foothills of the Rocky Mountains east to Nova Scotia, and south to central Texas and central Florida. In fall this vast group of individuals passes south to winter in South America in the upper basin of the Amazon. A closely related kind, the yellow-green vireo (*Vireo flavoviridis*), that nests in the tropical zone from northern México south to central Panamá, also leaves its nesting ground in September and October, to join the red-eye in the great valley of the upper Amazon. A further population, the black-whiskered vireo, *Vireo altiloquus*, found from southern Florida through the West Indies, is also mainly migratory to this same winter home, though a few remain permanently in the Greater Antilles. We may theorize that here also there is some tie for this habit back to Pleistocene climatic conditions. This appears clear in the case of the red-eyed vireo, but obscure with the others, since the yellow-green and black-

whiskered vireos now nest in areas that are tropical. It seems possible that during the period of the Wisconsin ice sheet temperature conditions in these areas of the northern Tropics were so different that an annual migration was established, which now continues though there is no apparent present necessity for it.

In concluding this review it is pertinent to consider some general problems that may associate the avifauna with other factors recorded for the Pleistocene. Birds in their more recent history have been a conservative group since families and a number of generic groups, found in the living avifauna, were current early in the Miocene. It also appears that many modern species had completed the changes that brought them to their present osteological form by the close of the Pliocene so that their Pleistocene representatives, where these have been found, seem to be specifically the same as those we know today. It should be obvious that the paleornithologist is restricted to differences in form and size in his identifications of the bones he examines. Color, on which the ornithologist working with modern museum specimens depends so largely, is lacking, but it seems reasonable to hold that if bones of a dove from a Pleistocene deposit appear identical with those of a modern mourning dove, they may be identified as that species, listed as *Zenaidura macroura*, and considered coordinate with the living population.

There has been some tendency to consider various Pleistocene forms as directly ancestral to closely related living species so that the two groups are held to be merely two stages in a continuous line of descent. While this may be true in some instances, such matters require cautious consideration. A case in point is the Pleistocene coot *Fulica minor*, described from Fossil Lake, Oreg., and recorded from beds of Illinoian age in Florida. It differs in longer leg and shorter wing from the living American coot (*Fulica americana*), recorded also at a number of Pleistocene localities, and has been cited as directly ancestral to the modern species. When I recall the three closely similar, but distinct, species of coots of the genus *Fulica* that I found living together in marshy pools in eastern Argentina, I am prone to believe that fossil *minor* is related to living *americana* merely through some ancestral fulinine stock, probably Pliocene, from which several kinds of coots have come, rather than that the two represent different stages in a single ancestral line. A similar situation may have existed in other groups, e.g., in the golden eagles, in which the Pleistocene population has not yet been given a name.

There are to date only fragmentary data to indicate the status of the

North American avifauna at the beginning of the glacial period. It may be admitted without great argument that the 83 known species that have become extinct were living at the close of the Pliocene, though as yet remains of only five of them have been found in deposits of upper Pliocene age. Eight modern species have been identified from the same upper Pliocene time period. The eared grebe (*Podiceps caspicus*) has been found in the Ogallala formation of Sherman County, Kans.; the double-crested cormorant (*Phalacrocorax auritus*), the gallinule (*Gallinula chloropus*), and the mallard (*Anas platyrhynchos*), are known from the Hagerman Lake beds, of Idaho. The bufflehead (*Bucephala albeola*), the turkey (*Meleagris gallopavo*), the American coot (*Fulica americana*), and the mourning dove (*Zenaidura macroura*) come from the Rexroad formation of Meade County, Kans. It should be added that there is question as to the age of the Hagerman Lake beds. Some believe that they are younger than the Rexroad formation, which would place them near the Pliocene-Pleistocene boundary. Hibbard (1958, p. 11) allocates them to Aftonian or first interglacial time. Such a transfer would reduce the living species recorded from the Upper Pliocene to five.

Definite data from the Pleistocene come mainly from the latter part of that period. Brodkorb (1953) has attributed 7 living species from Alachua County in northern Florida to Sangamon interglacial time, immediately preceding the last advance of ice. In another paper (1957) he has listed 52 species, 4 of them extinct, from Marion County in north-central Florida that he attributes to the preceding Illinoian glacial stage. The three asphalt deposits of California are allocated by Hibbard (1958, p. 10) to Wisconsin time. The combined total for Rancho La Brea, McKittrick, and Carpinteria is 117 species, of which 98 are still living. From the Fossil Lake beds, also placed in the late Pleistocene, 60 species of birds are recorded, of which 45 are still extant. From three late Pleistocene deposits in southwestern Kansas 14 living species have been obtained.

While the available data at the present moment go back only to the upper levels of middle glacial time, the greater number of birds recorded are those living today. It is my own opinion that most of the species of our present avifauna had attained development by the beginning of the Pleistocene, and that the major changes since have come through extinction of numerous kinds. It is my further belief that modification of those still in existence has been mainly at the subspecific level. It seems probable that at the beginning of the Pleistocene the number of species within the limits assigned to our

American Ornithologists' Union check-list may have equaled that found now in modern México.

The future contribution of paleornithology to information on the Pleistocene will come through the discovery of many additional species, and of further details of geographic range. It would seem that the chronology of the Pleistocene time clock so far as the Animal Kingdom is concerned must rest mainly on the mammalian micro-faunas, with corroboration now and then from their avian companions.

SUMMARY

The modern avifauna of North America north of México includes 796 species of which 87 are of casual occurrence, and 12 have been introduced by man. Of the 697 kinds that constitute the normal population, 190 have been found fossil in the Pleistocene; 7 more are recorded in Cuba and Nuevo León, and the tropical wood rail is known from Florida. In addition, 83 extinct species have been described, giving a total of 281 as the avifauna now known in Pleistocene time.

The principal Pleistocene collections have come from Fossil Lake, Oreg., three asphalt deposits in California, and several localities in southwestern Kansas and Florida, all located in the nonglaciaded area.

The greater number of known fossil species belong in the orders Anseriformes, Falconiformes, Galliformes, Gruiformes, and Passeriformes. The list includes representatives of 56 of the 72 families of North American birds, those lacking being mainly those with species of such small size that fossil remains are difficult to find, or of marine distribution for which few deposits are known.

The manner of range extension following retreat of the ice sheets is indicated by recent population spread toward the north of several kinds of birds in Finland, Iceland, and Greenland during rising annual temperatures of recent years. Climatic changes during the retreat of the Wisconsin ice sheet are believed to have set the pattern of annual migration for modern birds.

Close similarity between such species as the Pleistocene coot (*Fulica minor*) and the living American coot (*Fulica americana*) found fossil in the upper Pliocene as well as in the Pleistocene denote related forms descended from a common Pliocene ancestor rather than two stages in a single linear line of descent.

Eight modern species have been recorded from Upper Pliocene beds (if the three found in the Hagerman Lake beds are included as of that period).

It is believed that most of the species of the living avifauna were

present by the beginning of Pleistocene time, with evolution since, in the main, in characters at the subspecies level.

The further contribution of paleornithology to the Pleistocene record will be in the discovery of additional extinct species and in further record of living forms. Details of chronology for the various levels of the Pleistocene will depend mainly on the mammals.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 138, NUMBER 5

(END OF VOLUME)

A BIOLOGICAL SURVEY OF
KATMAI NATIONAL MONUMENT

(WITH 17 PLATES)

By

VICTOR H. CAHALANE

Formerly Chief Biologist, National Park Service

U. S. Department of the Interior



(PUBLICATION 4376)

CITY OF WASHINGTON

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PL. 1.—Dakavak Lake lies between 2,000-foot spurs of the Aleutian Range on the eastern slope of Katmai National Monument. The heavy deposit of volcanic ash has been partially covered by green alder and grasses. Snowy Mountain (elevation 7,142 feet) appears through the clouds about 18 miles away. Photographed July 28, 1953.

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A BIOLOGICAL SURVEY OF KATMAI NATIONAL MONUMENT

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(WITH 17 PLATES)

I. INTRODUCTION

HISTORY OF THE KATMAI REGION

Near the base of the Alaska Peninsula in southwestern Alaska is a wild and—by some standards—inhabitable region. I have been privileged to live in this unspoiled wilderness and to study its plant and animal life for three field seasons, a total of seven months. Despite rain, fog, and storms, it has a unique charm and fascination. With the exception of the most spectacular center of volcanic phenomena—a comparatively restricted area—most of the region is little known. Because of this, as well as my own deep regard for the country, I am presenting here a more ample account of it than might suffice for the cursory background of a biological study.

Apparently the Katmai region has never supported more than a few small villages of native people. Little is known about the aboriginal inhabitants, but presumably most of them were nomadic and followed the salmon runs, caribou, and other shifting sources of livelihood. Semipermanent settlements probably existed at or near the mouths of principal streams where the people harvested and stored supplies of the teeming hordes of migratory salmon. The only remaining evidences of these Aleut-Eskimo are a few grassy mounds and circular depressions on stream banks and ridges. These hummocks and holes are the only traces of their middens and barabaras, or sod huts.

Even the more sedentary folk of these villages must have roamed about at times, particularly when food became scarce or uncertain. Except in the area immediately around each settlement, they had little effect on the country, its vegetation or its wildlife. By comparison with the mighty brown bear, whose broad feet made trails in the tundra moss that endured for decades, their tracks were puny. Much of their

travel was by skin boat, or bidarka, on the inland lakes or the coastal waters of the Pacific Ocean. Their land routes, mostly along the margins of streams too turbulent for boats, were quickly overgrown when use ceased.

Aboriginal existence was devoted largely to the processes of survival—hunting and fishing. It was marked by periods of famine and times of plenty, and by raids and counterraid of rival Aleut-Eskimo tribes. The coming of the Russians in the mid-eighteenth century may not have been as disastrous to these Katmai people as it was to the inhabitants of the Aleutian Islands and other regions. Since Katmai had little or no natural wealth of gold and furs, it did not attract the attention of the rapacious "Lords of Alaska."

Purchase of Alaska by the United States was followed in 1899 by the discovery of gold at Nome. The trail across the Peninsula via Katmai Pass and Naknek Lake suddenly became a major travel route. It enabled the gold seekers to reach Bering Sea in three or four days' time and in relative safety, instead of making the long, uncertain and often dangerous voyage through the passes of the Aleutian Islands. A trading post was built at Katmai Village, near the outlet of Katmai River into Shelikof Strait, to meet the most essential needs of these prospectors. With the possible exception of three or four tiny Russian Orthodox churches, the trading post at Katmai Village probably was the first structure in the area to be built by whites.

As the beach sands at Nome were panned out, few travelers used the trail across Katmai Pass. Most of these were natives en route to visit relatives in villages across the Aleutian Range, or trappers with furs to sell at some distant trading post. Then in June 1912 the centuries-old track through the wilderness was destroyed in a most spectacular debacle.

A week of increasingly severe earthquakes was only the prelude to an awesome series of events. Beginning on June 6 and continuing for about 60 hours, the area around Mount Katmai was racked and convulsed by earth forces of tremendous magnitude. One effect of internal pressure was to blow enormous amounts of ash and pumice out of Novarupta, a relatively insignificant volcano located about 6 miles southwest of Katmai.

Almost simultaneously with the thunderous eruption of Novarupta a series of glowing avalanches of sand mixed with hot gases burst out of numberless fissures in the head of the valley west of Katmai Pass. Rushing down with incredible speed, these avalanches buried the floor of the valley, 3 to 6 miles wide and 15 miles long, to a depth up to 700

feet. The body of tuff consolidated, but it was perforated by countless fissures through which steam and gases escaped from the hot mass. These millions of fumaroles later gave the area its name which became known throughout the world—the Valley of Ten Thousand Smokes.

More than 7 cubic miles of rock and pumice were spewed onto the surface or into the atmosphere. So much material was ejected from the conduits leading to Novarupta and nearby fissures that a great cavity formed under Mount Katmai and the upper third of the mountain collapsed. Thus the crater, almost 3 miles across and 3,500 feet deep, was formed. A mass of andesite lava and cinders erupted on the caldera floor, forming a small cone. Eventually a lake accumulated, covering the cone beneath hundreds of feet of turquoise-blue water.

Gradually, the eruptions became less violent and finally ceased. There was no sound except the hiss and puff of fumaroles and an occasional “boom” from the depths of a crater. No living thing remained in the great steaming valley. On the Pacific side of the Pass an occasional bird flitted across a vast area east and southeast of Katmai Volcano, where the windblown ash had settled in depths up to 10 feet or more. Miles from the volcano only the sturdier shrubs and the lowland trees emerged from the pale buffy covering. Even these were festooned and broken by the load of fine pumice.

Apparently no human life was lost in this, one of the greatest eruptions in recorded history. The natives fled in fright and settled beyond the limits of the ash fall and possible new catastrophes. The Katmai region was deserted until in 1915 explorations were begun by the National Geographic Society.

Starting as a botanical study to investigate the recovery of vegetation following volcanism, the expeditions shifted attention to geological and volcanic work with the discovery in 1916 of the Valley of Ten Thousand Smokes. Seven expeditions were sent by the Society between 1912 and 1930, the last six under the able leadership of Dr. Robert F. Griggs. The personnel of the parties varied from 2 or 3 to 19. While most of the scientists were geologists, geophysicists, and chemists, botany was represented on at least one expedition by as many as four workers (Griggs, Jasper D. Sayre, Paul R. Hagelbarger, and D. B. Church); zoology by one (James S. Hine), and entomology by one (B. B. Fulton). (Hine also made a large collection of insects which included numerous species new to science.) A vast amount of information was accumulated and made known to the world through the National Geographic Magazine and in more technical

papers. From 1918 to 1923 Mount Katmai and the Valley of Ten Thousand Smokes was the most thoroughly studied and most widely publicized wild area in northwestern North America.

As a result of the National Geographic Society's work through 1917, and the first adequate description of the Valley of Ten Thousand Smokes, Katmai National Monument was created by proclamation of President Woodrow Wilson on September 26, 1918. The area included approximately 1,700 square miles, or more than a million acres. Following the last two expeditions, which widened knowledge of the scenic and biological resources of the region, the Monument was greatly enlarged by President Herbert Hoover's proclamation of April 24, 1931. The revised boundaries included more than 4,200 square miles. The Monument thus became by far the largest unit in the United States National Park System, and one of the largest scenic and wildlife reserves in the world.

A second modification, which added a relatively small acreage, was made by proclamation of President F. D. Roosevelt on August 4, 1942. This action extended protection to numerous islands and islets in the bays and within 3 miles of the coast of Shelikof Strait. Control of these islands was especially useful in preventing their use as bases for poaching on the furbearers and other wildlife of the mainland. This final extension of the boundaries brought the area of the Monument to its present (1959) total of 4,215 square miles, or about 2,697,600 acres.

ADMINISTRATION AND PROTECTION PROBLEMS

Because of its remoteness from routes of surface travel, Katmai National Monument was visited by very few people prior to World War II. Scientific studies were limited to the work of the National Geographic Society, and the final expeditions were made in 1923 and 1930. "Tourist travel," to use the professional phrase, was almost nonexistent. The trip to the Valley of Ten Thousand Smokes was costly in terms of both money and physical effort. At best, the journey through the alders and across the marshy slopes, rushing streams, and treacherous quicksand beds was rugged. For those lacking experience and know-how, it was dangerous.

Furthermore, it became evident as early as 1919 that the temperature of some fumaroles was dropping and that many of the smaller "smokes" were dying. Within a few years the activity had been greatly reduced. The highly scenic character of the region outside of the devastated areas was not widely known or appreciated, so public

interest declined with the assumption that the Monument contained little to justify its continued existence. Funds for protection of the wildlife from poaching were not available. Trappers hunted beaver, marten, and fox for furs, and moose for food, while commercial fishermen shot the great brown bears in vindictive retaliation for their feeding on salmon.

Even the National Park Service had little first-hand knowledge of this, its most far-flung responsibility. From the establishment of the Monument in 1918 until the end of World War II in 1945, three representatives of the Service visited the area. The "pioneer," Chief Ranger Louis M. Corbley of Mount McKinley National Park, was able to spend only a few hours at Brooks River about 1937, while Superintendent Frank Bean of McKinley Park and the writer traveled more widely for almost 6 weeks in 1940.

During the War considerable sport fishing was done at Brooks River by military personnel, and it was rumored that the larger trout were being depleted. With the return of peace and with the widespread use of aircraft by civilian hunters and fishermen in Alaska, fear arose that unrestricted use would be made of the wildlife resources of the Monument. Furthermore, organized interests started a campaign to "unlock" this vast, "idle" area and throw it open to exploitation. Some of the citizens of Naknek, a small community about 35 miles west of the Monument, petitioned for return to the public domain of all the area except the volcanic regions and the snowfields and glaciers. The petitions alleged that all other portions of the sanctuary were essential for private use of the fish, game, and fur and of the agricultural resources. It became essential for the Federal Government, as the custodian of a large public property, to determine the validity of these claims and the case for and against retention of the park. An extensive "inventory" was required.

THE KATMAI PROJECT

Early in 1953 the National Park Service submitted to the Office of Naval Research a proposal for a comprehensive investigation of natural phenomena in Katmai National Monument. The program, as it was approved and carried out during the following field season, included studies of (1) geographic and climatic conditions; (2) shore morphology; (3) geology, mineral resources, and glacier action; (4) volcanic activity, current and past; (5) human use of the area prior to the 1912 eruption; and (6) plant and animal life.

The natural history section of the Project, during the 1953 season,

was divided into three parts: (1) animal diseases communicable to man, which was carried out by Everett L. Schiller of the U. S. Public Health Service; (2) medical entomology, by Dr. William C. Frohne, also of the Public Health Service; and (3) an inventory of the plant and animal (bird and mammal) resources of the Monument, by the writer.

The Project was resumed in 1954 and additional studies were made under Sections 3 (geology and mineral resources); 4 (volcanic activity); 5 (past use by man); and 6 (plant-animal life). By force of circumstances the work in biology during the second season was confined to my own inventory of the biological resources. Plans of Messrs. Frohne and Schiller to resume work in the Monument for a brief period in early spring were revised. Since ice conditions prevented them from landing near Brooks River, they selected a site outside of the area. During the 1954 season the Project assisted a sport-fishery study on inland waters of the Monument by Dr. John Greenbank, an employee of the Fish and Wildlife Service.

My field research in the Katmai Project commenced on June 28, 1953, and was suspended September 14. It was resumed June 29, 1954, and concluded September 5. Acknowledgments for assistance are made in the introductions to the three sections of this report, and at other points in the text. I want especially to thank the following persons in the National Park Service: Ben H. Thompson, who coordinated the arrangements and management of the expeditions and kept them operating despite many difficulties; George L. Collins, who was largely responsible for suggesting the Project; and Robert S. Luntz, Project Leader, who worked indefatigably and efficiently as field manager to keep us supplied with all essentials for living in the wilderness and carrying out our research. I want to thank my assistant in the 1954 season, George B. Schaller, then a student at the University of Alaska, who was a companion and able packer and who contributed many valuable observations and plant specimens. Appreciation is also expressed for funds, transportation, equipment, and supplies to the U. S. Navy (particularly the Office of Naval Research), the Army, Air Force, National Park Service, Geological Survey, Public Health Service, and the Arctic Institute of North America. I hope that the information obtained through their support and recorded in the following pages will prove useful to these agencies.

For typing the manuscript, thanks are due Miss Ann Gorman of the National Park Service and Mrs. Mary K. Stearns of the New York State Museum and Science Service.

DESCRIPTION OF THE AREA

As was mentioned previously, Katmai National Monument embraces approximately 2,697,600 acres or 4,215 square miles—more than twice the size of the State of Delaware. The Monument is situated on the base of the Alaska Peninsula in southwestern Alaska. Its geographic center is 250 miles southwest of Anchorage, the largest city in the State. Access to the Monument formerly was by boat via Seward, 180 miles to the northeast, or from Kodiak, about 80 miles air-line distance to the east. During recent years, practically all travelers have entered the Monument from the commercial-military airport at King Salmon, 20 miles west of the western boundary.

The boundaries describe a rough parallelogram, 80 miles east and west by 50 miles north and south, with a 30-mile extension northeast to include the Cape Douglas region. The north side of the latter region is the western shore of Kamishak Bay on Cook Inlet. The boundary from Cape Douglas southwestward for 100 miles air line is formed by the west shore of Shelikof Strait. Rising steeply from the Strait, the Aleutian Range sweeps in an unbroken chain 20 to 30 miles wide from Mount Douglas on the north to Mount Martin near the southwestern boundary. Thence to the end of the Peninsula, the Range breaks into isolated peaks which are connected only by low ridges and foothills.

The central mass of the Aleutian Range is thus included within Katmai Monument. In comparison with many other mountain chains in Alaska the Aleutian Range is not among the most massive. It is, however, beautiful and impressive, particularly when viewed from Shelikof Strait. The highest elevation, Knife Peak (7,585 feet), stands a little apart from its neighbors and is a symmetrical cone-shaped mass. Four other mountains (Denison, 7,560 feet; Snowy, 7,142 feet; Douglas, 7,064 feet; and Mageik, 7,040 feet) exceed 7,000 feet in height. These and dozens of lesser points over a mile high rise to their full height only 5 to 10 miles from the sea. Within this mountain mass are at least 15 active, or recently active, volcanoes.

Mount Katmai is not the only typical example in the Monument of an exploded volcanic crater complete with its lake. Nearly 50 miles to the northeast, and about 7 miles west of Kaguyak, is a smaller but very striking rival. Almost unknown until about 15 years ago, the feature has been given the name Kaguyak Crater. (Pl. 2, fig. 1.) The eruption of this mountain occurred well before local history began, but as geologists rate time it was in the very recent past—perhaps as recently as a thousand years ago. The remaining stub of the mountain

is considerably lower than Mount Katmai, and its bare rocky slopes support no snowfields or glaciers. The crater is filled by a lake of blue water which is probably very deep. Two cinder cones break the surface; one is small, the other may rise 400 or 500 feet. The crater lip is roughly oval in outline. On the north side it rises in a towering, jagged cliff at least a thousand feet above the lake—a gigantic splinter that survived the collapse of the mountain into its hollowed-out center.

With the exception of a 5-mile interval west of Kaguyak, the main ridge of the Range from Mount Douglas to Mount Martin is snow covered throughout the year. The snowfields feed many glaciers, some of which are 3 to 4 miles wide and 10 or 12 miles long. The largest of these ice rivers may have jettisoned bergs directly into the sea as recently as a century ago, but now they are shrunk until the closest approach is 5 miles. In the latter instance, that of the Hallo Glacier, the ice front is stagnant behind a great terminal moraine only 300 feet above sea level. On the western slope of the range the lowest limit now attained by living ice (of the Hook Glacier) is more than twice that elevation.

The western slope of Mount Katmai supports a relatively small but complex series of glaciers which descend to the head of Knife Creek valley. Although much of the snowfield that feeds them was lost through the collapse of the mountaintop, these glaciers have been able to maintain their frontal positions with practically no change since 1912. Being thoroughly insulated by a 5-foot coating of volcanic ash, they have suffered little loss from melting.

Another remarkable glacier is *within* Katmai Crater. Obviously, this mass of snow packed into ice must have come into existence after the eruption that caused the mountain to collapse. This is the only glacier in the world the age of which is known.

A notable feature of the eastern side of the Monument is the series of beautiful bays which give variety to the coast. At the north and south are wide, shallow half-moons with sweeping curves of sandy beaches—Kaguyak, Hallo, and Katmai Bays. Back of the beaches are vast, wide valleys where the rivers flow gently through many creek-like channels and the land is marshy or, as in Katmai Valley, treacherous with quicksand. Between the open bays are the deep, narrow fiords which are named Amalik, Kinak, Missak, Kuliak, Kafliak, and Kukak Bays. They cut deep into the mountains—as much as 10 miles in the case of Kinak Bay. Their shores drop almost sheer into water hundreds of feet deep, and the slopes above reach for the sky with equal abruptness. In many places the mountains rise from the water at

more than 60-degree grades for over a thousand feet before bending backward toward their summits.

These rugged inlets, with their islands and sheer cliffs, are picturesque and fascinating. Deep blue water, great slopes of wind-drifted, pale buffy pumice, and patches of dark green alders make them highly colorful (frontispiece). The visitor is astonished at the cuplike Hidden Harbor, half a mile across and hundreds of feet deep, which is entered through a break in the cliffs hardly 100 feet wide. Few sights in Alaska can compete in quiet beauty with the island-dotted fiord of Amalik Bay and Geographic Harbor.

The western slope of the Aleutian Range descends more gradually than the eastern side, and with numerous long spurs and outpost mountains. Some of these mountains, 20 or even 40 miles from the crest of the Range, are 2,500 to 4,500 feet high. Among these out-riders are Mount Katolinat, Mount LaGorce, and Mount Dumpling (pl. 2, fig. 2). Even Sugarloaf Mountain, which is 70 air-line miles from the main crest and marks the northwestern corner of the Monument, rises 2,085 feet above sea level.

Numerous streams, many of them glacier fed, course down the valleys of the western slope. These waters join to form several good-sized rivers—the Rainbow, Savanoski, and Ukak. They are swift, turbulent streams which are braided (i.e., divided into numerous channels) and heavily loaded with rock dust and pumice. Some of them make radical changes in their courses from time to time. These and many lesser streams feed a series of large lakes which lie among the foothills and in the tundra region of the Monument.

This western and northwestern quarter of the area is the upper limit of the coastal plain which stretches away to the mud flats of Bristol Bay. Strictly speaking, the plain projects into the Monument only as the great fingers of Angle Creek valley and around the western portions of Brooks Lake and Naknek Lake. However, much of the hilly country south of Brooks Lake and north of the North Arm of Naknek Lake has the tundra-bog characteristics of the coastal plain without sharing its monotony. Indeed, the easterly two-thirds of the lake region is often considered the most beautiful section of the entire Monument. All of Grosvenor Lake and Iliuk Arm, the eastern part of Naknek Lake, and the Bay of Islands are largely or entirely hemmed in by massive mountains which rise as much as 3,000 feet above the waters. These lakes are deep and cold, and with one exception they are strikingly clear and blue. Iliuk Arm alone is yellowish gray, being colored by rock flour and volcanic ash from the Savanoski

and Ukak Rivers. The entire northwestern lake region of the Monument drains westward into Bristol Bay through the Naknek River. A relatively small area in the southwest, north and west of the summit of Mount Martin, is also on the Bristol Bay watershed but is drained by the King Salmon River.

The true coastal plain region of the extreme western Monument is below the 500-foot contour. The smooth, rolling hills are scattered helter-skelter so that the drainage is very irregular and poor. The country is dotted with ponds and lakes and coursed by sluggish, widely meandering streams. Frost-wedge cracks have been observed in places on the coastal plain within the Monument, so it is likely that permafrost exists under the higher or eastern portions of the plain.

CLIMATE

Although much less foggy, cloudy, and windy than the Aleutians, the Katmai region has a rugged climate. Perhaps it can be described as being about midway between the foul weather of those Islands and the not always enjoyable climate of the Alaskan mainland. Temperatures, wind velocity readings, and other climatic information for the Monument are either lacking or too fragmentary to be reliable. However, Will F. Thompson, Geographer of the Katmai Project in 1953, has estimated that the warmest monthly mean temperatures for lowland areas are in the vicinity of 55° F., while the winter mean fluctuates from 14° to 28° F. The annual precipitation is unknown, but it probably ranges between 20 and 80 inches depending on location. The Pacific slope receives the maximum amount while areas west of the Aleutian Range are considerably drier. (Luntz, 1954, pp. 26-49.)

In my personal experience during three field seasons the summer months were rainy and overcast. "Perfect" weather can be expected on a few days—perhaps a dozen or two—at irregular intervals through June, July, and August. At these times of continuous sunshine with only a few high clouds, the earth hums with activity and the landscape is magnificent in its green beauty. The rest of the days are wholly or partially overcast, when the sky is covered with a dense cloud ceiling ranging in height from 2 miles down to 1,000 feet or lower. Some precipitation will be recorded on the majority of these overcast days. It may be only a "trace," with heavy mist and drizzle for an hour or two during the night or a brief, light shower in the daytime. Occasionally a driving rain may continue for many hours, but most of the summer precipitation occurs as prolonged drizzle,

or showers alternating with periods of complete cessation. The effect is to keep the vegetation wet and the traveler complaining more or less irritably. During rainy periods the temperature is generally around 60° F. with little variation between day and night. On sunshiny days the thermometer registers in the seventies or occasionally low eighties during the day and in the fifties at night. Around eastern Naknek Lake light frost may occur rarely in August, but the first freeze is generally about September 5.

These comments are generalizations. Occasionally a summer occurs when "Aleutian weather" extends eastward over the entire Alaska Peninsula and even partially sunny days are rare. The opposite can also come about, as in June and July, 1953, when the Katmai area was blessed with more than 6 weeks of almost unbroken fine weather. During this period the temperatures on several occasions ranged between 85 and 90° F.

The traveler can usually depend on better weather, or at least less rain, the farther he goes westward from the Aleutian Range. More clouds and drizzle occur near the Range, and particularly around the Cape Douglas peaks and the Katmai-Mageik summits.

In fall a period of fair weather may be expected for 10 days to 3 weeks sometime in September and early October. Residents of the Naknek area claim that a similar period occurs in May and perhaps early June. Little information is available concerning the weather in the Monument during the colder months of the year. I have been told that temperatures in midwinter usually do not drop under minus 20° F., and that the large bodies of water such as Naknek Lake freeze over in November. Except for a few floes, the lakes were completely open by April 20, 1953. Snow depths in areas 20 to 30 miles west of the Aleutian Range usually do not exceed 2½ feet.

Although not as vital as in the Aleutian Islands, wind is an important climatic factor which affects plant and animal life of the higher altitudes in Katmai Monument. No actual measurements of wind velocity have been made here, but speeds in excess of 100 miles per hour undoubtedly are reached on the mountaintops and in passes through the Aleutian Range. Prior to the eruption of 1912, when the transmountain trail was in use, foot travelers regarded Katmai Pass as a particularly hazardous section because of the cold, violent winds. It was said that, even in summer, the natives did not dare to cross the Pass except in calm weather, for strong gusts were capable of blowing rocks along the ground and even through the air. Undoubtedly these stones were punice "bombs" from ancient eruptions and were

comparatively light, but they certainly were dangerous when blown by winds of high velocity. In this and other high-altitude areas of the region, strong winds sweep away the soil and smaller stones, and beat the larger particles into a firm, consolidated mass. The vegetation is molded and controlled by the blasts, and woody shrubs such as willow and alder are restricted to ravines and other depressions or are forced to assume a prone position. Exposed ridges are stripped of snow during the winter and the moisture available to plants on such sites is correspondingly reduced.

LIFE ZONES—WILDLIFE HABITATS

The Monument is the meeting ground of two life zones. The Arctic zone extends from the mountaintops downward to approximately 2,000 feet elevation. It may also reach considerably lower in the heads of some valleys where glaciers or other factors exert a cooling influence. At Katmai large areas of this zone along the main ridge of the Aleutian Range are covered by snowfields and glaciers.

Outside the limits of permanent snow and ice the Arctic zone is a simple one from the standpoint of the plant and animal life. The species are relatively few in number and are restricted to those types which are capable of resisting low temperatures, strong winds, aridity, and desiccation. The plants are low-growing forms, often with thick, leathery or pubescent foliage. They have extensive root systems which can obtain nourishment and anchorage in the coarse residual soils. The most abundant or more conspicuous plants of the Arctic zone are *Stereocaulon paschale* (a rock-growing lichen); mosses such as *Dicranum fuscescens*, *Racomitrium canescens*, and *Pohlia cruda*; *Lycopodium clavatum* (running club moss); *Poa arctica* (Arctic blue grass) and *P. hispidula* (hispid blue grass); *Carex* (sedge, several species); *Salix anglorum* and *S. alaxensis* (felty-leaved willow); *Betula nana* (dwarf alpine birch); *Oxyria digyna* (mountain sorrel); *Saxifraga flagellaris* (flagellate saxifrage) and *S. serpyllifolia* (thyme-leaved saxifrage); *Dryas octopetala* (eight-petaled mountain avens); *Oxytropis* (three species); *Rhododendron camtschaticum* (Kamchatka rhododendron); *Artemisia arctica* (Arctic wormwood), and *Arnica lessingii* (arnica). Birds of this zone include the American gyrfalcon, Nelson's rock ptarmigan, northern common raven, western water pipit, gray-crowned rosy finch, Alaska Lapland longspur, and snow bunting. The Arctic ground squirrel (*Spermophilus undulatus ablusus*), Arctic hare (*Lepus othus poadromus*), and several mice of the Cricetidae group are resident mammals, but the Peninsula



1. Kaguyak Crater (see pp. 7-8). Aerial view from the southwest. Beyond the crater rim is Big River and, on the center horizon, Four-peaked Mountain (elevation 6,903 feet). The lake in the caldera is about $1\frac{3}{4}$ miles long. Cliff on east (right) rim towers 1,800 feet above the water. August 26, 1954.



2. View east from summit of Mount LaGorce (3,183 feet). At far right of Iliuk Arm (lake in foreground) are the vast pumice delta of Ukak River and Mount Ikagluik. In left distance, Savanoski River winds from Hook Glacier on Mount Denison, Kukak Volcano, and Devils Desk (on left horizon). August 22, 1953.



1. Typical view in white-spruce forest east of Brooks River. Covering extensive areas on the western slope of the Mounment, it is the habitat of red squirrel, spruce grouse, three-toed woodpecker, and white-winged crossbill. August 2, 1954.



2. Marsh-bog habitat about 1 mile north of the outlet of Brooks River. The predominant plants are beaked sedge, horsetail, bog moss, cotton grass, sweet gale, swamp willowherb, and buckbean, with mixed thickets of willows, Kenai birch, green alder, and scattered white spruce and cottonwood. July 6, 1953.



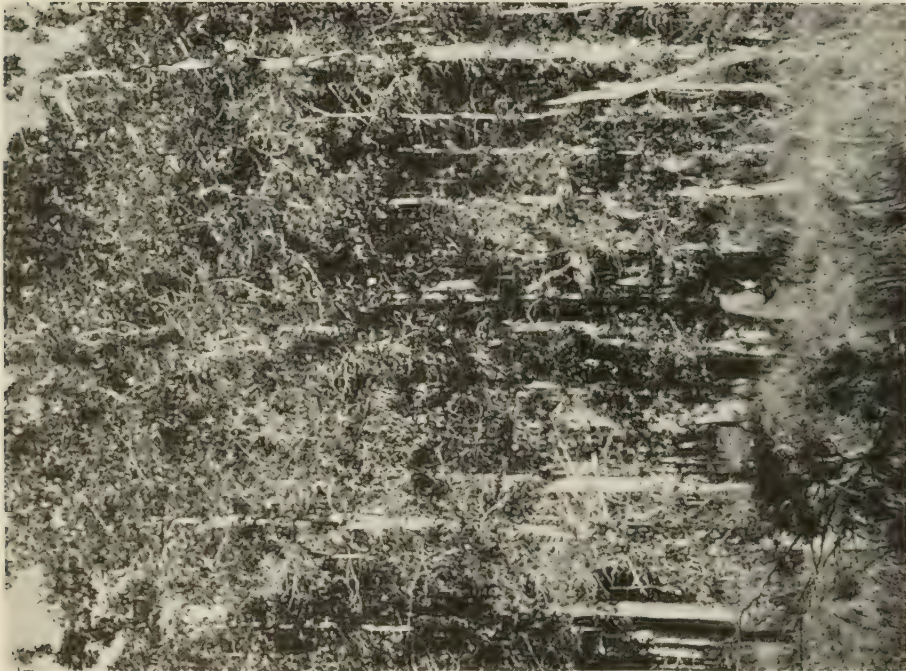
1. The low tundra (elevation up to 1,200 feet) is dotted by ponds and clothed by grasses, sedges, Mertens rush, many-flowered and hairy wood rushes, thin-capsuled willowherb, bog rosemary, bog blueberry, and many other species. View south from Contact Creek to mountains of the Aleutian Range. September 5, 1954.



2. The high tundra extends upward from about 1,200 feet above sea level. Typical plant species are running club moss, crowberry, Lapland cornel, alpine azalea, mountain harebell, everlasting, and Arctic wormwood. Photograph made from an elevation of 2,050 feet, southwest to Mount LaGorce and Iliuk Arm (appearing faintly at left). September 5, 1953.



2. White cotton grass, a widely distributed sedge on sandy and grassy flats and in wet places. It occurs from sea level to 2,000 feet elevation, Missak Bay, July 24, 1953.



1. Grove of cottonwood or balsam poplar, north of Iliuk Arm. The ground cover is luxuriant—sedges, bluejoint, lady fern, and numerous herbs such as white hellebore, cucumber-root, starflower, and bedstraw. August 20, 1954.



2. *Seacost angelica*, a rather common and conspicuous plant of grassy areas from sea level to 1,500 feet elevation. When mature, it was eaten by brown bears. Alagogshak Creek, July 28, 1953.



1. Dwarf fireweed was a pioneer species on the dry gravel ridges and pumice flats at the head of Knife Creek. The species was widespread in the Monument on open, grassy areas as high as 2,400 feet above sea level. Head of Knife Creek, July 10, 1953.



1. The ripe fruit of mooseberry, a common shrub of the low-altitude woodlands and thickets, was eaten by brown bears. (See p. 166.) Savanoski, September 1, 1953.



2. One of several small "islands" of vegetation (lower left) in the valley between Knife Creek and Mount Katmai. Here, apparently, life had survived the eruptions of 1912 and subsequently. Of 15 plant species, 8 were not found elsewhere in the Valley of Ten Thousand Smokes. (See pp. 71-72.) August 7, 1954.

brown bear, wolverine, interior Alaska wolf, and Alaska moose wander through the Arctic zone or come into it seasonally to forage for food.

Below the Arctic zone is the Hudsonian zone, which comprises the remaining and somewhat larger area of the Monument. Its deeper and richer soils, higher year-long temperatures, absence of snowfields and occasional summer hailstorms, and relative freedom from gales make it better adapted to support a great variety of plant and animal species. The terrestrial habitats are diversified, at least in comparison with the tundra habitat of the Arctic life zone. They range from the extensive white spruce (*Picea glauca*) forests of the lowlands around Iliuk Arm, Brooks Lake, and eastern Naknek Lake, groves of balsam poplar (*Populus tacamahaca*) which are in many stream-bottoms and on low-altitude slopes, thickets of green alder (*Alnus crispa*) and many species of willow (*Salix*), and extensive stands of grasses which often are mixed with the above-named deciduous trees and shrubs. Among the most important grasses and grasslike plants are *Calamagrostis canadensis* (bluejoint), *Agrostis scabra* (tickle grass), *Poa arctica* (Arctic blue grass) and *P. hispidula* (hispid blue grass), *Carex macrochaeta* (Alaska long-awned sedge) and *C. microchaeta*. Other conspicuous herbs and flowering plants of these habitats are too numerous to mention here.

The assemblage of birds which populate the Hudsonian zone, at least in summer, is particularly diversified. Ducks of many species are common, and whistling swans nest in the marshes. Loons, grebes, gulls, and shorebirds such as sandpipers, oyster-catchers, turnstones, and plovers are plentiful in the lakes region and along the seacoast. The marine environment also has murre, murrelets, guillemots, and puffins. The inland birds include birds of prey (hawks and owls), two grouse (Alaska spruce grouse and Canadian willow ptarmigan), woodpeckers, ravens and jays, thrushes, warblers, and sparrows.

While the mammalian fauna is not rich in species, it is more varied than in many other northern regions, and the large, conspicuous forms are numerous in respect to individuals. The most characteristic mammals of the Hudsonian zone are the Peninsula brown bear (*Ursus gyas*), the world's largest carnivore; wolverine (*Gulo luscus*); otter (*Lutra canadensis*); red fox (*Vulpes fulva*); interior Alaska wolf (*Canis lupus pambasileus*); lynx (*Lynx canadensis*); red squirrel (*Tamiasciurus hudsonicus kenaiensis*); beaver (*Castor canadensis*); varying hare (*Lepus americanus*), and Alaska moose (*Alces gigas*).

The map (fig. 4) at the back of the book will be useful to the reader in locating the mountains, lakes, collecting stations, and other points mentioned throughout the text. All names of topographic features and localities conform with the rulings of the U. S. Board of Geographic Names and are included in the most recent editions of U. S. Geological Survey quadrangles, with the 11 exceptions cited below. Several of these informal names, such as Savanoski and the Narrows, are widely used in the region. Other names were adopted by me or by other investigators of the Katmai Project staff because of the need to describe localities of significance in our research which had no authorized names. These informal place names are:

- Coville RiverThe short stream connecting Lake Coville with Grosvenor Lake.
- Cozy LakesA group of ponds, lat. $58^{\circ}13' N.$, long. $155^{\circ}58' W.$, around which Muller collected numerous species of plants. (See p. 16.)
- Iliuk MoraineSouth of Iliuk Arm and west of Margot Creek, at $58^{\circ}26' N.$ and $155^{\circ}38' W.$, where Muller made some plant collections.
- Knife Creek Glaciers...Numbered, for convenience by geologists of the Katmai Project, I to VI from west to east (counter-clockwise) as viewed from the upper valley of Knife Creek.
- Kukak PointThe peninsula on the north side of the entrance to Kukak Bay from Shelikof Strait.
- NarrowsThe water connection between Naknek Lake and Iliuk Arm.
- Red Top Mountain....A conspicuous mass that rises from the southwest shore of Grosvenor Lake to an elevation of 2,480 feet above sea level at $58^{\circ}38' N.$ and $155^{\circ}13' W.$ Plant collections were made here in 1919 by A. E. Miller of the National Geographic Society expedition. Apparently the place name was used only by this group.
- Research BayA shallow bay on the south shore of Iliuk Arm, west of the outlet of Margot Creek.
- SavanoskiSite of the village on the south bank of lower Savanoski River, abandoned in 1912.
- UkakSite of a small village or rest stop on the east side of Ukak River about 5 miles south of Savanoski, destroyed by the eruption of 1912.
- Whiskey RidgeA sharp promontory of Jurassic sandstone between Knife Creek Glaciers III and IV; the name was applied by Dr. Howel Williams and adopted by other geologists of the Katmai Project.

II. THE VEGETATION

An attempt was made to collect specimens of all species of plant life. For several reasons, this objective was not by any means attained. Time was not available for thorough collecting, especially at the higher elevations. The restricted period of fieldwork—late June to early September—undoubtedly caused the omission of some early-flowering plants which become inconspicuous later in the season. Some species, especially among the lower plants, probably were overlooked. Specialists in some of the lower plant groups, particularly the lichens, mosses, and fungi, may be able to add considerably to the portions of the following list in their respective fields.

HISTORY OF VEGETATION SURVEYS

In compiling the list of plants, time has not permitted me to review the literature for the purpose of including forms which were collected within Katmai National Monument by earlier workers. Considerable study has been given by botanists of the National Geographic Society to the vegetation of those areas which were most affected by the volcanic eruption of 1912. We also have record of two earlier, although very brief, explorations. Georg Heinrich von Langsdorff, Russian Consul-General in Rio de Janeiro, and Wilhelm G. Tilesius visited Kukak Bay July 27-29, 1806, and made collections of the plant life (von Langsdorff, 1812-1813). Presumably, the results, if still extant, are in Moscow. A brief stop for collecting was made in Kukak Bay on July 1, 1899, by Frederick V. Coville, Thomas H. Kearney, Jr., William Trelease, and others of the Harriman Expedition to Alaska; their specimens are in the Smithsonian Institution.

The most extensive work was done from 1915 to 1919 by fieldworkers of the National Geographic Society. Robert F. Griggs and his associates collected plants as follows: Griggs, July 19, 1915, at Soluka Creek; July 26-28, 1915, in Katmai Valley; Griggs and Donovan B. Church, July 19 and August 5, 1916, at Soluka Creek; Griggs with Paul R. Hagelbarger and Jasper D. Sayre, summer of 1917, Kashvik Bay and Katmai River valley as far as Katmai Pass; Hagelbarger and Sayre, August, 1918, along Naknek River, Naknek Lake, Iliuk Arm, and Ukak River valley; Griggs, et al., June-July, 1919, regions around head of Naknek Lake, Savanoski, Ukak, and Red Top Mountain. The collections of Griggs and his coworkers were deposited at Ohio State University, with duplicates in the U. S. National Herbarium. (See Griggs, 1915, 1918, 1919a, 1919b, 1922, 1933, 1934; Griggs et al., 1920; and Griggs and Ready, 1934.)

A small collection of plants was made at Idavain Lake, north of the North Arm of Naknek Lake, on June 27, 1950, by Karl A. Raup of the U. S. Geological Survey. This completes the history of botanical work in Katmai National Monument, as far as it is known to me, up to the beginning of the Katmai Project in June 1953.

All available records of plant collections made up to 1940 in the area now known as Katmai National Monument are given in Hultén's "Flora of Alaska and Yukon." Brief mention of some of these records has been made in the list that follows. However, such references are fragmentary and have been included only to expand the data on certain species which were collected in 1953 and 1954.

COLLECTING, 1953 AND 1954

During the first season, June 28 to September 15, 1953, I obtained approximately 500 field collections of plants. They represent 42 families, 117 genera, and 164 species. Included was a first authentic record for Alaska—*Catabrosa aquatica* (water hair grass), which was collected July 17, 1953, at Savanoski Village site about three-quarters of a mile above the outlet of the Savanoski River.

Dr. Ernest H. Muller, a geologist of the U. S. Geological Survey, who was making stratigraphic and geomorphic studies of glacial deposits in the Naknek Lake and Angle Creek areas and glaciological studies in the Knife Creek drainage, made incidental collections of plants in those areas on July 5, 6, 8, 10-13, 15, and 18, 1953. Dr. Muller accumulated 118 field collections of plants. They included representatives of 4 families, 5 genera, and 25 species which were not obtained by me. Information on this collection, together with that obtained by Raup in 1950, was generously made available and has been included in the annotated list. The addition of Muller's results, together with 1 genus and 6 species which were only in Raup's collection, materially increases the value of my list; for this, grateful acknowledgment is made. Numbers collected by Muller and Raup, with ecological data contributed by the former, are credited to the person responsible in each instance.

My botanical activities of the second season, June 29 to September 5, 1954, fell into two categories. First, a study of plant succession and recovery was begun by establishing five permanently marked plots in the Valley of Ten Thousand Smokes. (See pp. 72-73.) Second, I endeavored to extend collecting to new localities as well as to search for additional species in areas which had been covered the previous year. About 400 numbers were accumulated during this second season

for a 2-year total of 912. The work of 1954 resulted in adding 19 families of plants which consisted of 77 species in 32 genera. Thus the additional activity resulted in a sizeable addition to our knowledge of plants in the Monument.

Specimens collected by me have been deposited in the herbarium of the Smithsonian Institution, with duplicates being set aside for Mount McKinley National Park and Katmai National Monument. All plants bearing the collection numbers of Messrs. Muller and Raup have been turned over by the U. S. Geological Survey to the Smithsonian Institution.

The entire list, including the collections of Muller and Raup, comprises 65 families, 155 genera, and 273 species of plants. The distribution of the species by plant groups is as follows: Algae, 2; fungi, 3; lichens, 7; mosses, 19; ferns and their allies, 10; and flowering plants, 232.

COLLECTING STATIONS

Fairly complete collections of plants were obtained at the following 26 stations. Altitudes are given in feet above sea level. These ranged from sea level to 2,400 feet. The stations of Dr. Muller and Mr. Raup are indicated.

West base of Baked Mountain. Pumice flats and outwash slope. Elevation 2,000 ft. August 6, 1954.

West spur of Broken Mountain. Pumice ridges. Elev. 2,400 ft. August 6, 1954.

North base of Broken Mountain. Outwash gentle slope above Knife Creek.

Mostly pumice; numerous small washes. Elev. 2,000 ft. August 6, 1954.

Between Broken Mountain and Baked Mountain. Pumice valley. Elev. 2,400 ft. August 6, 1954.

Brooks River. Valley bottom. Willow-alder-cottonwood-spruce thickets and grassy meadows. Elev. 50 ft. July 8-15, August 15, 31, 1953; August 1-2, 14-31, 1954.

1 mile west of mouth of Brooks River. Lake border and slope. Cottonwood grove with alder-willow-spruce. Elev. 100 ft. August 15, 1953; July 26, 31-August 2, August 14-31, 1954.

East end of Lake Coville. Flat, low gravel spit. Cottonwood grove. Elev. 110 ft. July 5-24, 1954.

North and south shores of Lake Coville. Several stations. Mixed alder-willow-cottonwood-spruce thickets and woods. Elev. 110-300 ft. July 7-9, 16, 18, 1954.

Coville River. Swift stream and quiet bay; water 2 to 6 ft. deep. Elev. 107 ft. July 5-24, 1954.

Mount Dumpling. North and east slopes. Tundra merging into alder thickets. Elev. 1,200 to 2,000 ft. July 9-11, 1953.

Crest of Mount Dumpling. Gentle to steep slopes. Tundra grassland. Elev. 2,000 to 2,440 ft. July 9-11, 1953; August 2, 1954.

- North and south shores of Grosvenor Lake. Several stations. Mixed alder-willow-cottonwood-spruce thickets and woods. Elev. 110-300 ft. July 6, 12, 17, 18, 22, 24, 1954.
- Idavain Lake and immediate vicinity. Marshy flat and dry ridges and hillsides. Grass; alder and willow thickets. Elev. 700 ft. June 27, 1950 (Raup).
- Islet north of Research Bay, near southwestern shore of Iliuk Arm. Small, rocky island. Grass; willows and alder. Elev. 40 ft. July 16, 1953.
- 5 miles northwest of Kaguyak. Flat above river channel. Mixed thickets; cottonwood grove; brushy opening. Elev. 50 ft. July 24, 1953.
- Upper Katmai Canyon. Pumice ridge. Elev. 1,000 ft. July 28, 1953.
- Katmai River. Rocky ridge in flat valley, about 2 miles north of Katmai Bay. Grass, alder thickets. Elev. 50 ft. July 25, 28, 1953.
- Head of Katmai River. Pumice ridge. Elev. 2,000 ft. July 28, 1953.
- Head of Knife Creek. Gravel ridges in broad, pumice-covered valley below west slope of Katmai Volcano. Elev. 2,000-2,200 ft. July 20-21, 1953; August 5-9, 1954.
- Upper Knife Creek at east base of Knife Peak. Steep, rocky canyon. Rocky bluff and steep grass-covered slope. Elev. 2,400 ft. August 7, 1954.
- Kuikpalik Island. Grassy flat. Elev. 130 ft. July 29, 1953.
- Ridge between Kukak and Kafia Bays. Gentle to steep north slope. Grass with alder thickets. Elev. 1,500 ft. July 28, 1953.
- Kukak Bay (4 localities). Flats and ridges. Alder-willow thickets; grass. Elev. sea level to 130 ft. July 23-August 10, 1953.
- Kuliak Bay. Rocky peninsula at head of bay. Spruce grove bordered by alder thickets and grass. Elev. 50 ft. July 11, 1954.
- South rim of Novarupta. Pumice ridge. Elev. 2,500 ft. August 8, 1954.
- Savnoski and vicinity (numerous localities). Old river dune, mixed woods, small stream. Spruce-cottonwood-alder-willow, and grass. Elev. 60-100 ft. July 17-20, August 19-28, 1953 (Cahalane); July 12, 1953 (Muller).
- Junction of Ukak and Savnoski Rivers. Gravel delta with seeps and small flowing streams, largely barren. Elev. 35 ft. July 17-20, August 19-28, 1953.

Incomplete Stations

Incomplete collections varying in size from a few plants to considerable numbers were made at 42 localities which ranged in elevation from sea level to 7,589 feet. These samplings were limited because generally only one visit was made to the spot, usually by helicopter or other aircraft, and the time that could be afforded was short.

- Alagogshak Creek. Valley bottom. Willow-alder thickets; grassy openings; cottonwood forest. Elev. 50-100 ft. July 25, 28, 1953.
- Lower American Creek, 2 to 3 miles west of Lake Coville. Valley bottom. Alder-grass and marsh. Elev. 125 ft. July 18, 1954.
- Mouth of American Creek. Open grass and mud flat. Elev. 110 ft. July 18, 1954.
- Off mouth of American Creek, west end of Lake Coville. Water 1 to 3 ft. deep. Elev. 105 ft. June 18, 1954.
- Angle Creek, 58°13' N., 155°24' W. Steep, rocky hills north of creek. Elev. 1,200 to 2,000 ft. July 10, 1953 (Muller).

Angle Creek, $58^{\circ}13' N.$, $155^{\circ}27' W.$ Braided outwash, valley train deposits and isolated low gravel knolls. Elev. 800 ft. July 11, 1953 (Muller).

Bay of Islands. Low, rounded hills. Alder–willow thickets. Elev. 100 ft. August 15 and 25, 1954.

South shore of Naknek Lake, North Arm, northwest of summit of Mount LaGorce. Mixed woods, under 20 ft. high, with swift stream. Elev. 100 ft. August 15 and 25, 1954.

1 mile east of mouth of Brooks River. Alder–willow–spruce on moraine. Elev. 100 ft. July 31, August 14, 1954.

1 mile north of mouth of Brooks River. Mixed woodland and marsh. Elev. 100 ft. July 8-15, August 14, 1953; July 26, 1954 (Cahalane); July 17, 1953 (Muller).

Contact Creek, 6 miles above junction with Takayoto Creek. Grassland with ponds; hills with grass and alder thickets. Elev. 600-1,000 ft. September 5, 1954.

2 miles southwest of Lake Coville. Gentle rolling terrain; bog. Elev. 250 ft. August 17, 1953.

Cozy Lakes, $58^{\circ}13' N.$, $155^{\circ}58' W.$ Steep mountain slopes on rubble soils, and alluvial slopes at foot of mountain. Elev. 600 to 2,900 ft. July 15, 1953 (Muller).

Cape Douglas. Flat promontory on Shelikof Strait. Grassy tundra. Elev. 25 ft. July 29, 1953.

Rocky hill between Falling Mountain and Novarupta. Slide fragments in pumice outwash plain. Elev. 2,400 ft. August 8, 1954.

Geographic Harbor. Steep pumice slopes. Alder thickets and small grassy openings. Elev. 100 ft. July 24, 1953.

3 miles north of west end of Grosvenor Lake. Steep mountain slope. Grass and alder thickets. Elev. 2,000 ft. August 17, 1953.

Hallo Bay. Broad, flat beach and outwash plain. Grass and spruce forest with alder fringe. Elev. 25 ft. August 4, 1953; July 11, 1954.

Northeast of Hidden Harbor. Pumice slopes and steep ridges. Elev. 2,500 ft. July 26, 1953.

2 miles north of Idavain Lake. Rolling, stony terrain. Grassy tundra; stunted alder; dwarf birch and willow. Elev. 1,500-2,000 ft. August 29, 1954.

Northwest and northeast shore of Iliuk Arm of Naknek Lake (two stations). Rocky lake shore, sloping gently back to steep mountainside (Mount LaGorce). Mixed woodland and thickets. Elev. 50-300 ft. August 2 and 18, September 1, 1954.

South shore of Iliuk Arm (two stations). Sand and gravel beach; beach dune. Elev. 50 ft. August 15, 1953; August 21, 1954.

Iliuk Moraine, south of Iliuk Arm, $58^{\circ}26' N.$, $155^{\circ}38' W.$ Flood plain of Margot Creek and low moraine knolls. Cottonwood–willow–alder. Elev. 200-250 ft. July 13, 1953 (Muller).

Kafkia Bay. Peninsula; rocky slopes and sandy flat. Grass; alder thickets. Elev. sea level to 50 ft. July 11, 1954.

5 miles northwest of Kaguyak Crater. Mountain slopes. Elev. 2,500 ft. July 23, 1953. (Small collection made by Werner Juhle; no ecological data.)

South fork of Kamishak River. Valley bottom; rocky soil. Cottonwood grove and alder–willow thickets; grassy meadows. Elev. 650 ft. September 3, 1953.

- Mount Katolinat. Steep, rocky north slopes on arkosic conglomerate and gray-wacke. Elev. 1,500-2,700 ft. July 13, 1953 (Muller).
- Kinak Bay. Wide pumice flat at head of bay. Cottonwood groves; alder thickets; open grass and pumice flats. Elev. 50-100 ft. July 24, 1953.
- Head of Knife Creek, 200 ft. from Fourth Glacier ($58^{\circ}16'$ N., $155^{\circ}05'$ W.). Pumice-mantled apron near toe of Fourth Glacier. Elev. about 2,200 ft. July 5, 6, and 8, 1953 (Muller). (This station includes a portion of "Head of Knife Creek," collected by Cahalane.)
- Knife Peak. Steep ash slope and pumice flat on crest. Scant grass. Elev. 7,500 ft. August 4, 7, 1954. (Collection by George B. Schaller.)
- 5 miles northwest of Kukak Crater. Steep, almost barren ridge. Elev. 2,500 ft. July 23, 1953. (Collection by Werner Juhle.)
- 2 miles south of Kukak Volcano. Almost barren ridge crest. Elev. 4,500 ft. July 26, 1953.
- Mountain south of Kulik Lake. Elev. about 2,000 ft. June 27, 1950 (Raup; no ecological data; outside of Monument).
- Missak Bay. Flat, gentle slope and ravine. Alder, grass. Elev. 50-100 ft. July 24, 28, 1953.
- 3 miles southeast of Murray Lake. Rolling tundra in shallow valley of small stream. Grass; willow-alder thickets. Elev. 2,000 ft. September 5, 1953.
- 2 miles east of Naknek (outside of Monument). Rolling, brushy tundra with groves of cottonwood. Elev. 100 ft. June 30, 1954.
- South shore of Naknek Lake at west boundary of Monument. Broad, gentle sloping ridge; north slope and crest. Elev. 300 ft. August 17, 1954.
- 2 miles north of mouth of Savanoski River. Rolling hills in flat marsh. Mixed woodland; bog. Elev. 100 ft. August 16, 1953.
- 2 miles southeast of mouth of Savanoski River. Outwash plain. Willow-alder-spruce. Elev. 150 ft. August 16, 1953.
- Swikshak Lagoon. Flat marsh and grassy dunes. Elev. 10-20 ft. August 4, 1953.
- Takli Island, Amalik Bay. Rolling; gentle slopes. Grass; alder thickets, and pumice flat. Elev. 10-30 ft. July 24, 28, 1953.
- Mouth of Ukak River. West bank; dunes and flats. Open pumice, marshes, beaver ponds, and grass. Elev. 100 ft. August 2, 1954.

ACKNOWLEDGMENTS

Appreciation has been expressed for permission to use the collections which were made by Ernest H. Muller and Karl A. Raup of the U. S. Geological Survey. Plants were brought to me in the field by other members of the Katmai Project, particularly by Dr. Werner Juhle and Donald Williams in 1953 and by George B. Schaller, my assistant in 1954.

All my plant collections were identified by others, and I want to acknowledge the great assistance thus rendered on the various groups of plants by the following persons: algae—Francis Drouet, Chicago Natural History Museum; fungi—Calvin E. Higgins, of Eli Lilly and Company, Indianapolis; lichens—Alexander W. Evans, professor-

emeritus of Yale University, Mackenzie Lamb, of Harvard University, and Grace E. Howard, of Wellesley College; mosses—William C. Steere, New York Botanic Garden, and E. B. Bartram, of Bushkill, Pike County, Pa.; ferns and allies—C. V. Morton, Smithsonian Institution; Gramineae—Jason R. Swallen, Smithsonian Institution; Cyperaceae—F. J. Hermann, Bureau of Plant Industry; Salicaceae—the late Carleton R. Ball, U. S. Department of Agriculture; all other groups by E. H. Walker, Smithsonian Institution. I am especially grateful to Dr. Swallen, Dr. Walker, Mr. Morton, and others of the Department of Botany, Smithsonian Institution, for advice and other help in carrying out the botanical section of my assignment.

Nomenclature and format of my manuscript were checked by Eugene C. Ogden and Stanley J. Smith of the New York State Museum and Science Service. Their review resulted in numerous improvements and is gratefully acknowledged.

EXPLANATORY NOTES

The following accounts of species include the scientific and vernacular names, the type of habitats in which each species was found growing, the lowest and highest elevations above sea level, and the localities in the Monument where collections were made. If specimens of a given species were obtained from more than five habitats and localities, the terms "widespread" and "numerous localities," respectively, are used instead of enumerating a lengthy list.

Field numbers are listed following the record of localities. Numbers from the collections of Muller and/or Raup are identified by the addition of those collectors' names in parentheses; all other numbers are those of the writer.

The month and day on which specimens were collected are given in sequence for each species. If collections were made on more than five dates, however, the record is abbreviated by showing the total number of instances and the first and last dates on which the species was obtained.

In many cases notes on the flowering or fruiting condition are appended as well as statements concerning the relative scarcity or abundance of the plants. When available, short comments on the usefulness of the plants for food or medicinal purposes are given. This information, as well as notes on preparation for consumption or use and warning against taking poisonous species, has been summarized chiefly from Heller's "Edible and Poisonous Plants of Alaska," 1953.

In most cases, the nomenclature of the pteridophytes and sperma-

tophytes follows Hultén's "Flora of Alaska and Yukon" (1941-1950), and the sequence of genera is that of Gray's "Manual of Botany" (1950 edition). For the lower plants, the authority for sequence of genera is Engler's "Syllabus der Pflanzenfamilien" (1954). Common or vernacular names for the vascular plants are from J. P. Anderson's "Flora of Alaska and Adjacent Parts of Canada" (1943-1952).

LIST OF PLANT SPECIES

CYANOPHYTA (Blue-green algae)

OSCILLATORIACEAE

1 genus; 1 species

Symploca muralis Kütz. Habitat: throat of active fumarole. Elevation 2,000 feet. Locality: west base of Baked Mountain. No. 909. August 6. A fairly extensive area about 5 feet below the mouth of the fumarole was coated with this alga. The temperature at times rose to 80° C. Dr. Garniss Curtis supplied this reading and the following comment: "I took temperatures at several places where I observed the alga growing and found that it does not occur where the temperature is much above 80° C. I suspect that the temperature of optimum growth is somewhat lower than 80° C., but am fairly certain that the alga can stand this high a temperature for at least short periods of time—perhaps only seconds." (Personal communication, March 2, 1955.)

Samples of alga from the largest fumarole at the south base of Baked Mountain were collected July 21, 1953, and submitted for identification to Dr. Francis Drouet of the Chicago Natural History Museum. He reported that the specimen was "beyond recognition, having been overgrown by fungi and together having formed an incipient lichen—which is too young for determination in this group." (Letter to Dr. Jason R. Swallen, April 28, 1954.)

CHLOROPHYTA (Green algae)

PRASIOLACEAE

1 genus; 1 species

Schizogonium murale Kütz. Habitat: rocks in waterfall. Elev. 2,400 ft. Upper Knife Creek, east base of Knife Peak. No. 910. August 7.

ASCOMYCETES (Ascus fungi)

ASPERGILLACEAE

2 genera; 3 species

Aspergillus niger van Tieghem, forma. Habitat: throat of active fumarole. Elev. 2,000 ft. Southwest base of Baked Mountain. July 21.

Aspergillus sydowii (Bain. & Sart.) Thom & Church. Habitat: throat of active fumarole. Elev. 2,000 ft. Southwest base of Baked Mountain. July 21.

Penicillium purpurogenum Stoll. Habitat: throat of active fumarole. Elev. 2,000 ft. Southwest base of Baked Mountain. July 21.

LICHENES (Lichens)

SPHAEROPHORACEAE

1 genus; 1 species

Sphaerophorus fragilis (L.) Pers. Habitat: spruce-willow-birch bog. Elev. 150 ft. Portage between Bay of Islands and Grosvenor Lake. No. 906b. July 17.

CLADONIACEAE

2 genera; 5 species

Cladonia alpestris (L.) Rabh. Habitat: spruce-willow-birch bog. Elev. 150 ft. Portage between Bay of Islands and Grosvenor Lake. No. 905. July 17.

Cladonia metacorallifera Asahina. Habitat: spruce-willow-birch bog. Elev. 150 ft. Portage between Bay of Islands and Grosvenor Lake. No. 906. July 17. Known also from northern Alaska and southern South America.

Cladonia mitis Sandst. Habitat: "tundra" near birch-cottonwood scrub. Elev. 100 ft. 2 miles east of Naknek. No. 907. June 30.

Cladonia squamosa (Scop.) Hoffm. forma *muricella* (Del.) Vainio. Habitat: spruce-willow-birch bog. Elev. 150 ft. Portage between Bay of Islands and Grosvenor Lake. No. 906c. July 17.

Stereocaulon paschale (L.) Hoffm. subsp. *alpinum* (Laur.) Mont. Habitat: ridge crest. Elev. 2,500 ft. 5 miles northwest of Kukak Crater. No. 888. July 23. A northern lichen that occurs chiefly on rocks.

PARMELIACEAE

1 genus; 1 species

Parmelia centrifuga (L.) Ach. Habitat: spruce-willow-birch bog. Elev. 150 ft. Portage between Bay of Islands and Grosvenor Lake. No. 908. July 17.

BRYOPHYTA (Mosses)

DICRANACEAE

1 genus; 1 species

Dicranum fuscescens Turn., fuscous dicranum. Habitat: dry tundra. Elev. 2,700 ft. Mount Katolinat. Muller 1224. July 13. Plants were "growing in areas of late snowdrift, but parched" at time of collection (Muller).

GRIMMIACEAE

1 genus; 1 species

Racomitrium canescens Brid. Habitat: ridge crest. Elev. 2,500 ft. 5 miles northwest of Kukak Crater. No. 887. July 23.

BRYACEAE

2 genera; 4 species

Pohlia cruda (Hedw.) Lindb. Habitat: rock. Elev. 6,500 ft. Knife Peak. No. 895. August 5.

Pohlia rothii (Correns) Brotherus. Elev. 50 ft. Missak Bay. No. 892. July 24.

Pohlia wahlenbergii (W. & M.) Andrews. Angle Creek, 58°13' N., 155°24' W. Muller 1175. July 10.

Bryum caespitium Hedw. Elev. 50 ft. Missak Bay. No. 891. July 24. Grows on earth, dry banks, stones.

MNIACEAE

1 genus; 2 species

Mnium affine Bland. Habitat: cottonwood grove. Elev. 100 ft. $\frac{1}{4}$ mile west of mouth of Brooks River. No. 900b. August 14.

Mnium medium Bruch & Schimper. Habitat: wet grass-willow flat. Elev. 150 ft. North shore of Lake Coville. No. 896. July 7.

AULACOMNIACEAE (Bog moss family)

1 genus; 1 species

Aulacomnium palustre (W. & M.) Schwaegr., bog moss. Habitat: bog, wet grass-willow flat. Elev. 150-250 ft. North shore of Lake Coville; 3 miles southwest of Lake Coville. Nos. 889, 897, 898. July 7, August 17. Occurs in swampy woods and bogs from the Arctic south over much of the United States.

BARTRAMIACEAE (Apple moss family)

1 genus; 1 species

Philonotis fontana (Hedw.) Brid., philonotis. Habitat: moist, rocky bluff. Elev. 2,400 ft. Upper Knife Creek, east base of Knife Peak. No. 899. August 7.

CLIMACIACEAE (Tree moss family)

1 genus; 1 species

Climacium dendroides (Hedw.) W. & M., European tree moss. Habitat: cottonwood grove. Elev. 100 ft. $\frac{1}{4}$ mile west of mouth of Brooks River. No. 900. August 14.

BRACHYTHECIACEAE

1 genus; 1 species

Brachythecium albicans (Hedw.) B.S.G. Habitat: ridge crest; cottonwood grove. Elev. 100-2,500 ft. $\frac{1}{4}$ mile west of mouth of Brooks River; 5 miles northwest of Kukak Crater. Nos. 886, 900a. July 23, August 14.

ENTODONTACEAE

1 genus; 1 species

Pleurozium schreberi (Brid.) Mitten. Habitat: spruce-birch-poplar-willow-alder woods. Elev. 100 ft. 1 mile west of mouth of Brooks River. Muller 1267. July 20.

HYPNACEAE

1 genus; 1 species

Ptilium crista-castrensis (Hedw.) DeNot. Elev. 100 ft. 1 mile west of mouth of Brooks River. Muller 1268. July 20.

HYLOCOMIACEAE

1 genus; 1 species

Hylocomium splendens (Hedw.) B.S.G., mountain fern moss. Elev. 100 ft. 1 mile west of mouth of Brooks River. Muller 1268. July 20.

POLYTRICHACEAE (Hair-cap moss family)

2 genera; 4 species

Pogonatum alpinum (Hedw.) Brid., alpine pogonatum. Habitat: pumice soil. Elev. 2,500 ft. Base of rocky hill between Falling Mountain and Novarupta. No. 901. August 8.

Pogonatum capillare (Michx.) Beauv. Habitat: rock. Elev. 6,500 ft. Knife Peak. No. 902. August 5.

Polytrichum commune Hedw., hair-cap moss. Habitats: pumice; spruce-birch-poplar-willow-alder woods. Elev. 100-2,500 ft. Base of lava plug, Novarupta; 1 mile west of mouth of Brooks River; west of Savanoski Village site. Nos. 890, 903, Muller 1267. July 17, 20, August 6.

Polytrichum juniperinum Hedw., juniper hair-cap moss. Habitat: rock crevice. Elev. 2,500 ft. Rocky hill between Falling Mountain and Novarupta. No. 904. August 5.

PTERIDOPHYTA

POLYPODIACEAE (Wood fern family)

6 genera; 6 species

Woodsia ilvensis (L.) R. Br., rusty woodsia. Habitat: rock cliff, south side of island. Elev. 150 ft. Lake Coville, 2 miles northwest of Coville River. No. 735. July 8.

Cystopteris fragilis (L.) Bernh., brittle fern. Habitats: cliff near waterfall; shady rock bluff. Elev. 20-200 ft. North prong of Kukak Bay; east shore of Iliuk Arm 2 miles northwest of mouth of Savanoski River. Nos. 368, 402, 734. August 2, 5.

Dryopteris austriaca (Jacq.) Woyn., spinulose wood fern. Habitat: spruce forest. Elev. 50-500 ft. Hallo Bay; Idavain Lake. Nos. 394, 396, 403, Raup 338. June 27, August 4.

Gymnocarpium dryopteris (L.) Newm., oak fern. Habitats: spruce-hardwood woodland, usually spruce-cottonwood; grassy flat; valley bottom. Elev. 100-200 ft. Numerous localities, both east and west of Aleutian Range. Nos. 392, 405, 726, 727, 728, 729, 730, 731, Muller 1264. Seven dates, July 7-August 14.

Thelypteris phegopteris (L.) Slosson, long beech fern. Habitats: grassy flat; grassy openings between alder clumps; well-drained moraine knoll at edge of river, volcanic ash soil. Elev. 20-1,000 ft. Angle Creek 58°13' N., 155°27' W.; Kukak Bay; Kuikpalik Island. Nos. 388, 393, 406, Muller 1189. July 11, 29, August 3. "Not uncommon," Angle Creek (Muller).

Athyrium filix-femina (L.) Roth subsp. *cyclosorum* (Rupr.) C. Chr., lady fern. Habitats: wet swale; cottonwood grove. Elev. 20-2,000 ft. Mount Dumpling; $\frac{1}{4}$ mile west of mouth of Brooks River; Alagogshak Creek; Kukak Bay; Hallo Bay. Nos. 391, 395, 397, 398, 399, 400, 401, 404, 732, 733. July 11, 23, 28, August 3, 4, 14.

EQUISETACEAE (Horsetail family)

1 genus; 3 species

Equisetum arvense L., common horsetail. Habitats: widespread. Elev. 0-2,400 ft. Numerous localities. Nos. 370, 371, 372, 373, 374,

375, 377, 378, 379, 380, 381, 382, 383, 384, 385, 717, 718, 719, 720, 721, Muller 1157. Fourteen dates, June 29-August 17. A stabilizer plant on sandy and pumice soils.

E. arvense forma *alpestre* (Wahl.) Luer. Valley of Ten Thousand Smokes. Elev. about 2,000 ft. Muller 1156. July 5.

Equisetum fluviatile L. forma *linnaceum* (Döll) Broun., water horsetail. Habitats: bog, marsh, willow streamside, gravel beach. Elev. 100-300 ft. Three miles southwest of Lake Coville; south shore of Grosvenor Lake; 1 mile north of mouth of Brooks River; Research Bay, south shore of Iliuk Arm. Nos. 369, 376, 722, 723. July 15, 22, August 17, 22.

Equisetum sylvaticum L., wood horsetail. Habitat: ridge. Elev. 150 ft. South shore of Naknek Lake at western boundary of Monument. Nos. 724, 725. August 17.

LYCOPODIACEAE (Club moss family)

1 genus; 1 species

Lycopodium clavatum L. var. *monostachyon* Grev. & Hook., running club moss. Habitat: grass and scattered alder-willow shrubs. Elev. 2,000 ft. 3 miles southeast of Murray Lake. Nos. 386, 387. September 5.

SPERMATOPHYTA

PINACEAE (Pine family)

1 genus; 2 species

Picea glauca (Moench) Voss, white spruce. Habitat: old dune. 1 mile east of mouth of Savanoski River; 2 miles southeast of mouth of Savanoski River. Nos. 363, 365. August 22, 26. Common west of the Aleutian Range below the 1,000-ft. contour. The spruce forest is extensive east and south of Brooks Lake, where individual trees may grow to diameters of 12 inches or more. Scattered, stunted specimens exist at higher altitudes, being found on the summit of Mount LaGorce (3,183 ft.).

Picea sitchensis (Bong.) Carr., Sitka spruce. Elev. 75-100 ft. Iiallo Bay; north prong of Kukak Bay; south shore of Kukak Bay. Nos. 361, 362, 364, 366, 367. August 4, 5, 7. Small groves or lone

specimens grow at several localities in Kukak and Kuliak Bays. A few large trees on Takli Island in Amalik Bay, presumably killed by the ash fall of 1912, were still standing in 1954. Griggs stated that spruce were found in Katmai River Valley in 1915-1916. A considerable area (estimated in excess of 1,000 acres) on the southern flat east of Hallo Bay is covered with an old forest of Sitka spruce. Three of the larger trees, measured with a steel tape, were found to have circumferences of 68, 86, and 102 in. about 4 ft. above the ground.

ZOSTERACEAE (Pondweed family)

1 genus; 2 species

Potamogeton praelongus Wulfen, white-stemmed pondweed. Habitat: river bottom, 4 to 5 ft. depth. Elev. 107 ft. Coville River. Nos. 571, 572, 573. July 16.

Potamogeton vaginatus Turcz., sheathed pondweed. Habitat: lake bottom, water 2 ft. deep. Elev. 105 ft. Off mouth of American Creek, west end of Lake Coville. Nos. 850, 851. July 18.

JUNCAGINACEAE (Arrow grass family)

1 genus; 1 species

Triglochin maritimum L., seaside arrow grass. Habitat: grassy flat. Elev. 10 ft. Swikshak Lagoon. No. 201. August 4. Fruiting.

GRAMINEAE (Grass family)

12 genera; 22 species

Alopecurus acqualis Sobol., short-awned foxtail. Habitat: mud flat. Elev. 110 ft. Mouth of American Creek. No. 775. July 18.

Arctagrostis latifolia (R. Br.) Griseb., arctagrostis. Habitat: south slope. Elev. about 1,500 ft. 8 miles west of north end of Lake Coville. Nos. 261, 262. August 17. Fruiting.

Agrostis borealis Hartm., red bent grass. Habitats: sandy flat; pumice. Elev. 100-2,300 ft. Missak Bay; head of Katmai River. Nos. 214, 219. July 24, 28. Fruiting.

Agrostis scabra Willd., tickle grass. Habitats: dry bench; sand bar (?); wet seep in mud flow. Elev. 100-2,000 ft. Numerous locali-

ties. Nos. 210, 211, 213, 215, 217, 218, 231, 233, 237, 254, 258, Muller 1209. July 12, 17, 20, 24, 28. Fruiting. A grass probably belonging to this species was found August 15 growing on a gravel beach on the south shore of the North Arm of Naknek Lake, elev. 200 ft. No. 757.

A. scabra var. *geminata* (Trin.) Swallen, tickle grass. Habitats: moist rock bluff; dry ridge. Elev. 2,200-2,400 ft. Upper Knife Creek, east base of Knife Peak; head of north fork of Knife Creek; Valley of Ten Thousand Smokes. Nos. 754, 755, 756, 758, Muller 1151. July 5, August 4, 7. Fruiting.

Calamagrostis canadensis (Michx.) Beauv., bluejoint. Habitats: widespread. Elev. 25-2,700 ft. Numerous localities. Nos. 220, 222, 224, 226, 228, 230, 232, 235, 236, 238, 239, 240, 241, 242, 244, 247, 248, 249, 250, 251, 252, 253, 255, 259, 260, 736, 737, 738, 739, 740, 741, 742, 743, 744, 745, 746, 747, 748, 749, 750, 751, 752, 753, Muller 1194. 21 dates, July 7-September 6. Mostly fruiting. An abundant plant species. Utilization: A fair forage plant.

Muller noted that at 1,000-2,000 ft. on Angle Creek this species was growing on "a slope with *Epilobium angustifolium*, *E. latifolium*, *Equisetum*, a little *Salix* and *Alnus*, *Veratrum*, lupine."

Calamagrostis deschampsoides Trin., reed grass. Habitat: sand dunes. Elev. 25 ft. Swikshak Lagoon. No. 220. August 4. Fruiting.

Deschampsia caespitosa (L.) Beauv., tufted hair grass. Habitats: Small creek; wet seep in mud flow; ash slope; sandy flat. Elev. 100-2,700 ft. Numerous localities. Nos. 221, 223, 234, 256, 257, 769, 770. June 30; July 17, 21, 24, 28. Mostly fruiting, July 17-28.

Trisetum spicatum (L.) Richt., downy oat grass. Habitats: dry bench; dry ridge; wet seep in mud flow. Elev. 275-2,700 ft. Numerous localities. Nos. 212, 216, 227, 772, Muller 1153, 1220. Six dates, June 29-July 28. Fruiting, July 17-28. "Fairly common" at 2,700 ft. on Mount Katolinat (Muller).

Catabrosa aquatica (L.) Beauv., water hair grass. Habitat: small stream. Elev. 60-150 ft. Savanoski Village site. Nos. 243, 771. June 30, July 17. Fruiting.

The first authentic record of this species for Alaska.

Poa arctica R. Br. subsp. *williamsii* (Nash) Hult., Arctic blue grass. Habitats: ridges; alluvial flat. Elev. 2,000-2,200 ft. Numerous localities. Nos. 776, 777, 778, 779, 780, 781, 782, 783, 784, Muller 1160, 1221. June 29, July 6, 13, August 4, 6. Most fruiting. "Fairly common" on Mount Katolinat, July 13 (Muller).

P. arctica subsp. *longiculmis* Hult., Arctic blue grass. Habitat: reed grass meadow. Elev. 600 ft. Not abundant. Mount Katolinat. Muller 1228. July 13.

Poa eminens Presl, large-flowered spear grass. Habitat: grassy flat. Elev. 30 ft. Hallo Bay. Nos. 789, 790. July 11. Fruiting.

Poa glauca Vahl, glaucous spear grass. Habitat: rock cliff, south side of island. Elev. 120 ft. Lake Coville, 2 miles northwest of Coville River. Nos. 785, 786. July 8. Fruiting.

Poa hispidula Vasey, hispid blue grass. Habitats: dry bench; bank of small stream; wet seep in mud flow. Elev. 40-4,000 ft. Head of Katmai River; south rim of Novarupta; head of Knife Creek; junction of Ukak and Savanoski Rivers; 1 mile north of mouth of Brooks River; Savanoski. Nos. 203, 204, 205, 206, 207, 208, 209, 792. June 30, July 13, 17, 20, 21, 28. Fruiting.

Poa lanata Scribn. & Merr., lanate blue grass. Habitats: valley bottom; pumice flat. Elev. 2,000 ft. Between Broken Mountain and Baked Mountain. No. 791. August 6. Fruiting.

Poa paucispicula Scribn. & Merr., bog blue grass. Elev. 2,300 ft. Head of Katmai River. No. 202. July 28. Fruiting.

Poa pratensis L., Kentucky blue grass. Elev. 1,000 ft. Upper Katmai Canyon. No. 229. July 28. Fruiting. Introduced.

Poa stenantha Trin., narrow-flowered blue grass. Habitat: ridge. Elev. 2,200 ft. West spur of Broken Mountain. Nos. 787, 788. August 6. Fruiting.

Arctophila fulva (Trin.) Anders. Habitat: alder-grass river bank. Elev. 125 ft. Lower American Creek. Nos. 773, 774. July 18.

This species was collected from Red Top Mountain, July 21, 1919,

by Miller, and deposited in the U. S. National Herbarium. (Hultén, 1941-1950, vol. 2, p. 225.)

Glyceria borealis (Nash) Batchelder, northern manna grass. Habitat: marshy lagoon. Elev. 110 ft. North shore of Grosvenor Lake, 9 miles east of Coville River. No. 764. July 24.

Glyceria grandis S. Wats., American manna grass. Habitats: marshy lagoon, shallow water (2 to 3 ft.). Elev. 50-100 ft. Bay of Islands; north shore of Grosvenor Lake, 9 miles east of Coville River. Nos. 759, 760, 761, 762, 763, 765, 766. July 24, August 15.

Festuca rubra L., red fescue. Elev. 130 ft. Kuikpalik Island. No. 225. July 29. Fruiting.

Elymus mollis Trin., beach rye grass. Habitats: beaches and lake shores; grassy flat; seep in mud flow. Elev. 30-250 ft. Numerous localities. Nos. 245, 246, 263, 767, 768, 789. 6 dates, July 8-August 15. Fruiting.

CYPERACEAE (Sedge family)

2 genera; 16 species

Eriophorum angustifolium Honck., tall cotton grass. (Pl. 5, fig. 2.) Habitats: marsh; outwash plain. Elev. 100-2,000 ft. North base of Broken Mountain; 1 mile north of mouth of Brooks River. Nos. 200, 848. July 13, August 6. Fruiting.

Utilization: The basal 4 or 5 inches of the stem may be eaten raw. The underground stems are cached by mice and are edible; the black outer segments may be removed by dipping in boiling water.

Eriophorum scheuchzeri Hoppe, white cotton grass. Habitats: wet seep in mud flow; sandy flat; grassy flat; outwash plain. Elev. 40-2,000 ft. Missak Bay; Kuikpalik Island; junction of Ukak and Savanoski Rivers; Alagogshak Creek; north base of Broken Mountain. Nos. 196, 197, 198, 199, 849. July 17, 24, 28, 29, August 6. Fruiting.

Carex aquatilis Wahlenb., water sedge. Habitat: stony ridge (moraine). Elev. 1,000 ft. Contact Creek, 6 miles above junction with Takayoto Creek. No. 550. September 5. Fruiting.

Carex bigelovii Torr. & Schwein., Bigelow sedge. Habitats: well-drained moraine knoll at edge of river, volcanic ash soil; ridge. Elev. 100-2,700 ft. Angle Creek; Mount Katolinat; south shore of Naknek Lake at west boundary of Monument. Nos. 541, Muller 1188, 1227. July 11, 13, August 17. Fruiting. "Fairly common" on Angle Creek, 58°13' N., 155°27' W., July 11 (Muller). "Common" on Mount Katolinat, where associated (but not abundant) species were *Empetrum*, *Ledum*, *Loiseluria*, *Petasites*, *Arctostaphylos*, *Vaccinium uliginosum*. July 13 (Muller).

Carex canescens L., silvery sedge. Habitat: wet grass-willow flat. Elev. 100-200 ft. North shore of Lake Coville; Alagogshak Creek. Nos. 415, 569. July 7, 28. Fruiting.

C. canescens var. *disjuncta* Fern., silvery sedge. Angle Creek, 58°13' N., 155°24' W. Muller 1199. July 11.

Carex kelloggii W. Boott, Kellogg sedge. Habitat: small stream. Elev. 20-250 ft. Savanoski; Takli Island, Amalik Bay. Nos. 419, 567, 568. June 30, July 25. Fruiting.

Carex lugens Holm, sedge. Habitat: streamside, willows. Elev. 200 ft. 7 miles east of Coville River on south shore of Grosvenor Lake. No. 560. July 22. Fruiting.

Carex lyngbyei Hornem., Lyngbye sedge. Habitats: swales and moist flats; stream banks; sand bar. Elev. 20-250 ft. Numerous localities. Nos. 420, 421, 551, 552, 553, 554, 555, 556, 557, 558, 564, Muller 1208. 8 dates, June 30-July 25. Fruiting.

Carex macrocephala Willd., large-headed sedge. Habitat: beach dune. Elev. 20 ft. Hallo Bay. No. 570. July 11. Fruiting.

Carex macrochaeta C. A. Meyer, Alaska long-awned sedge. Habitats: dry ridges and benches; outwash plain. Elev. 20-2,000 ft. Takli Island, Amalik Bay; head of Knife Creek; Cape Douglas; north base of Broken Mountain; ridge between Kukak and Kaslia Bays; upper Katmai Canyon. Nos. 408, 409, 410, 412, 413, 429, 430, 549. 6 dates, July 20-August 6. Fruiting.

Carex mertensii Prescott, Mertens sedge. Habitats: dry flats and ridges; pumice; fumarole area. Elev. 2,000-3,000 ft. Numerous localities. Nos. 423, 424, 425, 426, 427, 428, 545, 546, 547, Muller 1159. 8 dates, July 5-August 8. Fruiting.

Carex microchaeta Holm, sedge. Habitats: "tundra"; andesite flows, volcanic ash soil (Muller). Elev. 2,000-2,700 ft. Mount Dumppling; 2 miles north of Idavain Lake; Mount Katolinat; Angle Creek, 58°13' N., 155°24' W. Nos. 539, 540, 548, Muller 1166, 1223. July 10, 13, August 2, 29. Fruiting.

"Abundant at 2,700 ft. on Mount Katolinat," July 13; "sparse" on Angle Creek, 58°13' N., 155°24' W., July 10 (Muller).

Carex nesophila Holm, Bering Sea sedge. Elev. 2,000-2,300 ft. Crest of Mount Dumppling; head of Katmai River. Nos. 414, 422. Fruiting. July 10, 28.

Carex nigrescens C. A. Meyer, blackish sedge. Habitat: volcanic ash soil. Angle Creek, 58°13' N., 155°24' W. Muller 1172a. July 10. "Fairly common" (Muller).

Carex rostrata Stokes, beaked sedge. Habitats: marshes, grass-alder streamside; cottonwood-alder swale; sandy beach; bluff. Elev. 50-300 ft. Alagogshak Creek; west end of Grosvenor Lake; lower American Creek; 1 mile north of mouth of Brooks River; $\frac{1}{4}$ mile east of mouth of Brooks River; mouth of Ukak River. Nos. 417, 418, 542, 543, 544, 561, 562, 563, 565, 566. 6 dates, July 5-August 19. Fruiting.

Carex subspathacea Wormsk., Hoppner sedge. Elev. 2,000 ft. 3 miles north of west end of Grosvenor Lake. No. 416. August 17. Fruiting.

JUNCACEAE (Rush family)

2 genera; 9 species

Juncus balticus Willd., Baltic rush. Elev. 100 ft. Alagogshak Creek. No. 192. July 28. Fruiting.

Juncus castaneus J. E. Sm., chestnut rush. Habitat: wet seep in mud flow. Elev. 40 ft. Junction of Ukak and Savanoski Rivers. No. 194. July 17. Fruiting.

Juncus falcatus E. Meyer, sickle-leaved rush. Elev. 1,500 ft. Mis-sak Bay; ridge between Kukak and Kafia Bays. Nos. 188, 189, 190, 191. July 24, 26. Fruiting.

Juncus filiformis L., thread rush. Habitat: bluff. Elev. 50 ft. Alagogshak Creek. No. 193. July 25. Fruiting.

Juncus mertensianus Bong., Mertens rush. Habitat: volcanic ash soils (Muller). Elev. 1,000-2,000 ft. Angle Creek, $58^{\circ}13' N.$, $155^{\circ}24' W.$ and $27' W.$ Muller 1169, 1172b, 1183, 1200. July 10, 11. "Not abundant" at $58^{\circ}13' N.$, $155^{\circ}27' W.$; "fairly common" at $58^{\circ}13' N.$, $155^{\circ}24' W.$, Angle Creek, July 10 and 11 (Muller).

Luzula arcuata (Wahlenb.) Wahlenb., alpine wood rush. Habitat: dry ridges. Elev. 2,000-2,700 ft. Head of Knife Creek; Valley of Ten Thousand Smokes; Mount Katolinit; north fork of Knife Creek. Nos. 534, 535, 536, 537, 538, Muller 1150, 1152, 1222. June 29, July 5, 13, August 4. Fruiting.

This species (probably) was collected by E. H. Muller, No. 1171, July 10, on andesite flows, volcanic ash soils. The plants were growing in a clump of *Campanula* on Angle Creek, $58^{\circ}13' N.$, $155^{\circ}24' W.$

Luzula multiflora (Retz.) Lejeune, many-flowered wood rush. Habitat: well-drained moraine knoll at edge of river, volcanic ash soil. Elev. 1,000-2,000 ft. Angle Creek, $58^{\circ}13' N.$, $155^{\circ}27' W.$ Muller 1191. July 11. "Common" (Muller).

Luzula parviflora (Ehrh.) Desv., small-flowered wood rush. Habitats: ash slope; dry bench; ridge top. Elev. 1,000-2,700 ft. Ridge between Kukak and Kafia Bays; Upper Katmai Canyon; east slope of Broken Mountain; head of Knife Creek. Nos. 182, 183, 184, 185, 186, 187. July 20, 21, 26, 28. Fruiting.

Luzula rufescens Fisch., hairy wood rush. Habitat: well-drained moraine knoll at edge of river, volcanic ash soil. Elev. 1,000-2,000 ft. Angle Creek, $58^{\circ}13' N.$, $155^{\circ}27' W.$ Muller 1193. July 11. "Fairly common" (Muller).

LILIACEAE (Lily family)

4 genera; 4 species

Tofieldia coccinea Richards., northern asphodel. Elev. 2,000 ft. 3 miles north of west end of Grosvenor Lake. No. 181. August 17. Fruiting.

Veratrum eschscholtzii A. Gray, American white hellebore. Habitat : wet swale. Elev. 100-2,000 ft. Cape Douglas ; Mount Dumphling. Nos. 179 (in flower), 180 (in bud), 836 (in flower). July 10 (in bud), July 29, August 2 (in flower).

Utilization: The plant contains several toxic alkaloids known to be fatal to sheep and other animals. The thick root or other parts should not be eaten.

Fritillaria camschatcensis (L.) Ker-Gawl., Indian rice. Habitats : grass-alder-spruce woods ; grassy flat ; streamside in cottonwood grove. Elev. 30-250 ft. North shore of Grosvenor Lake, 5 miles east of Coville River ; Hallo Bay ; Kuikpalik Island ; Kuliak Bay ; 5 miles northwest of Kaguyak. Nos. 177, 178, 841, 842, 843. July 11, 12, 24, 29. In flower, July 11, 12 ; fruiting, July 24, 29.

Utilization: The bulblets are edible fresh or dried. The liquid resulting from fermentation is intoxicating.

Streptopus amplexifolius (L.) DC., cucumber-root. Habitats : willow-alder-birch woods ; cottonwood grove ; opening in spruce forest. Elev. 50-300 ft. 1 mile west of mouth of Brooks River ; south shore of Grosvenor Lake, 8 miles east of Coville River ; $\frac{1}{4}$ mile west of mouth of Brooks River ; Hallo Bay. Nos. 174, 175, 176, 837, 838, 839, 840. July 22, 26, August 4, 14. Fruiting.

This species has sweet, edible fruits. The young tender shoots have a cucumberlike flavor and may be eaten raw.

IRIDACEAE (Iris family)

1 genus ; 1 species

Iris setosa Pall., wild iris. Habitats : grass-alder peninsula ; grassy flat. Elev. 30-100 ft. Hallo Bay ; Kafia Bay ; Alagogshak Creek ; Cape Douglas. Nos. 171, 172, 173, 844, 845, 846, 847. July 11 (in flower), 25 (in flower and fruiting), 29 (fruiting).

ORCHIDACEAE (Orchid family)

1 genus ; 1 species

Spiranthes romanzoffiana Cham. & Schlecht., hooded ladies-tresses. Elev. 60-250 ft. Cape Douglas ; Savanoski Village site. Nos. 168, 169, 170, Muller 1207. July 12, 17, 29. In flower.

SALICACEAE (Willow family)

2 genera; 18 species

Populus tacamahacca Mill., balsam poplar. Elev. 100 ft. 1 mile north of mouth of Brooks River; Savanoski. Nos. 167, Muller 1205, 1206. July 12, 13.

Utilization: The gummy balsam from the buds is useful as a salve for insect bites.

Salix alaxensis (Anders.) Coville, felty-leaved willow. Habitat: dry, gravel ridges. Elev. 2,000-2,200 ft. Head of Knife Creek, Valley of Ten Thousand Smokes. Nos. 4, 37, 38, Muller 1164. June 29, July 8, 20.

Utilization: The young new shoots and leaves are excellent sources of vitamin C. The inner bark in winter and spring is sweet and edible.

S. alaxensis var. *longistylis* (Rydb.) Schneider, felty-leaved willow. Habitat: gravel ridge. Elev. 2,200 ft. Head of north fork of Knife Creek. No. 13. August 4.

Salix anglorum Cham., willow. Habitat: dry ridge. Elev. 2,000-3,000 ft. Head of Knife Creek, Valley of Ten Thousand Smokes; Mount Katolinat; Cozy Lakes, 58°13' N., 155°58' W. Nos. 5, Muller 1161, 1215, 1259. June 29, July 5, 13, 16. In flower. "Common" to "abundant" (Muller).

Salix arbusculoides Ands. var. *glabra* Anders., willow. Habitat: dry bench. Elev. 2,000 ft. Head of Knife Creek. No. 39. July 20.

Salix arctica Pall., Arctic willow. Habitats: dry, stony ridges; "tundra"; outwash plain. Elev. 100-2,500 ft. Numerous localities. Nos. 15, 16, 26, 31, 42, 43, 44, 46, 47, 48, 49. 10 dates, July 10-September 6. Fruiting.

S. arctica var. *obcordata* (Anders.) Rydberg, Arctic willow. Habitats: "tundra"; ridges; "recent andesite flows, volcanic ash soils" (Muller). Elev. 50-2,500 ft. Numerous localities. Nos. 11, 12, 17, 18, 27, 40, 41, 45, Muller 1168. 7 dates, July 10-August 29. Fruiting.

Salix barclayi Anders., Barclay's willow. Habitats: dry, stony ridges; pumice flat; outwash plain; margin of small stream. Elev.

20-2,200 ft. Numerous localities. Nos. 1, 2, 7, 14, 30, 51, 52, 53, 54. 8 dates, June 29-September 6. In flower; fruiting.

Twigs of Collection No. 7 had been clipped (by *Microtus*-size rodent?).

Salix bebbiana Sargent, long-beaked willow. Habitat: beach in cove. Elev. 110 ft. North shore of Lake Coville, 6 miles northwest of Coville River. No. 9. July 8. In flower.

S. bebbiana var. *perrostrata* (Rydb.) Schneider, long-beaked willow. Habitat: willow-birch woods on ridges and hills. Elev. 150 ft. 5 miles northwest of Kaguyak; north shore of Lake Coville; south shore of Grosvenor Lake, 7 miles east of Coville River. Nos. 8, 10, 50. July 7, 22, 24. Fruiting.

Salix commutata Bebb, willow. Habitat: mud flow. Elev. 40-2,000 ft. Junction of Ukak and Savanoski Rivers; 3 miles north of west end of Grosvenor Lake. Nos. 55, 56. July 17, August 17. Fruiting.

One of the species revegetating the "mud flow" or delta of Ukak River.

Salix desertorum Richards., willow. Valley of Ten Thousand Smokes. Muller 1158. July 6.

Salix geyeriana Anders., willow. Habitat: head of Knife Creek, Valley of Ten Thousand Smokes. Muller 1163. July 8.

Salix glauca L. var. *glabrescens* (Anders.) Schneider, willow. Habitat: bluff. Elev. 50 ft. Alagogshak Creek. No. 57. July 25. Fruiting.

S. glauca var. *acutifolia* (Hook.) Schneider, willow. Habitat: ridge. Elev. 50 ft. South shore of Naknek Lake at west boundary of Monument. Nos. 19, 20, 21, 22, 23, 24. Fruiting.

No. 24 approaches *S. g.* var. *glabrescens* (Anders.) Schn. in broader, blunter leaves.

Salix ovalifolia Trautv., oval-leaved willow. Elev. 100-130 ft. Cape Douglas; Kuikpalik Island. Nos. 58, 59. July 29. Fruiting.

Salix phlebophylla Anders., willow. Habitat: dry tundra on old terrace, south side of lake. Idavain Lake. Raup 345. June 27.

Salix pseudomonticola Ball (? , juv.), willow. Habitat: dry ridge. Elev. 2,000 ft. Head of Knife Creek. No. 3. June 29. Early flowering stage.

Salix pulchra Cham., beautiful willow. Habitats: "tundra"; stony ridge; mixed spruce-alder-willow forest. Elev. 100-2,000 ft. 1 mile north of mouth of Brooks River; Idavain Lake; Contact Creek, 6 miles above junction with Takayoto Creek; 2 miles north of Idavain Lake. Nos. 28, 29, 32, 33, 34, 60, 61, Raup 346. June 27, July 10, 13, August 29, September 6.

Young stems, leaves, and underground shoots are edible raw and are excellent sources of vitamin C.

S. pulchra var. *palmeri* Ball, beautiful willow. Habitat: dry ridge. Elev. 1,000-2,000 ft. Head of Knife Creek; Mount Katolinat; Contact Creek, 6 miles above junction with Takayoto Creek. Nos. 6, 35, Muller 1226. June 29, July 13, September 6.

Salix reticulata L. var. *subrotunda* Seringe, willow. Elev. 2,000 ft. 3 miles west of north end of Grosvenor Lake. No. 62. August 17.

Salix scouleriana Barratt, willow. Habitats: ash slope; stony ridges. Elev. 50-2,700 ft. East slope of Broken Mountain; south shore of Naknek Lake at west boundary of Monument; Contact Creek, 6 miles above junction with Takayoto Creek. Nos. 25, 36, 63. July 21, August 17, September 6. Fruiting, August 17.

Salix sitchensis Sanson, Sitka willow. Elev. 100 ft. Missak Bay. No. 64. July 24.

MYRICACEAE (Wax-myrtle family)

1 genus; 1 species

Myrica gale L., sweet gale. Habitats: bog; wet marsh. Elev. 100 ft. 2 miles north of mouth of Savanoski River; 3 miles southwest of Lake Coville. Nos. 147, 148, 149, 150. August 16, 17. Fruiting.

CORYLACEAE (Hazel family)

2 genera; 4 species

Betula kenaica Evans, Kenai birch. Elev. 50-2,000 ft. 1 mile north of mouth of Brooks River; 5 miles northwest of Kaguyak; 3 miles

north of west end of Grosvenor Lake. Nos. 151, 152, 153. July 13, 24, August 17. No. 151 exhibited aberrant characters of a variety or hybrid.

Betula nana L. subsp. *exilis* (Sukatch.) Hult., dwarf alpine birch. Habitat: dry, stony ridges and hills. Elev. 100-2,000 ft. Numerous localities. Nos. 154, 155, 156, 829, 830, Raup 330. 6 dates, June 27-September 6.

Betula resinifera Britton, Alaska birch. Habitat: ridge. Elev. 100 ft. South shore of Naknek Lake at west boundary of Monument. Nos. 834, 835, 836. August 17.

Alnus crispa (Ait.) Pursh., green alder. Habitats: mud flow; edge of spruce forest. Elev. 50-275 ft. Hallo Bay; junction of Ukak and Savanoski Rivers. Nos. 164, 166. July 17, August 4. Fruiting.

One of the species revegetating the mud flow at mouth of Ukak River.

A. crispa subsp. *sinuata* (Regel) Hult., green alder. Habitats: widespread. Elev. 50-2,000 ft. Numerous localities. Nos. 157, 158, 159, 160, 161, 162, 163, 165, 831, 832, 833, Muller 1204. Fruiting.

POLYGONACEAE (Buckwheat family)

4 genera; 8 species

Koenigia islandica L., koenigia. Missak Bay. No. 526. July 24. In flower.

Rumex arcticus Trautv., Arctic dock. Habitat: cottonwood grove. Elev. 600 ft. Cozy Lakes, 58°13' N., 155°58' W.; northwest shore of Grosvenor Lake; Angle Creek, 58°13' N., 155°27' W. Nos. 834, 835, Muller 1195, 1247. July 5, 11, 16. Fruiting. "Fairly uncommon; 12-24 inches high" (Muller).

Rumex fenestratus Greene, great western dock. Habitat: wet swale. Elev. 2,000 ft. Mount Dumlup. No. 524. July 10. Fruiting.

Utilization: Young plants can be cooked for greens.

Oxyria digyna (L.) Hill, mountain sorrel. Habitats: dry benches and ridges; outwash plain. Elev. 500-2,700 ft. Numerous localities.

Nos. 525, 527, 528, 529, 530, 531, 826, 827, 828, Muller 1155, 1181, 1210. 8 dates, June 29-August 6. In flower, June 29; fruiting, August 24-September 4. Fairly abundant in the upper valley of Knife Creek; not common elsewhere.

Utilization: The leaves, eaten raw, are a good source of vitamin C.

Polygonum bistorta L. subsp. *plumosum* (Small) Hult. Habitat: tundra. Cozy Lakes, 58°13' N., 155°58' W. Muller 1234. July 15. "In dry *Empetrum* mat; 10-14 inches tall" (Muller).

Polygonum caurinum Robinson, Alaska knotweed. Habitat: sandy beach. Elev. 50 ft. Mouth of Brooks River. Nos. 814, 815, 816. August 19.

Polygonum oncillii Brenckle. Habitats: gravel beach; wet sandy beach. Elev. 50 ft. Small lake $\frac{1}{4}$ mile east of mouth of Brooks River; Research Bay, south shore of Iliuk Arm. Nos. 810, 811, 812, 813. August 19, 22. In flower.

Polygonum viviparum L., alpine bistort. Habitat: streamside in cottonwood grove. Elev. 100-200 ft. North shore of Grosvenor Lake, 5 miles east of Coville River; Cape Douglas; Cozy Lakes, 58°13' N., 155°58' W. Nos. 532, 533, 825, Muller 1251. July 12, 15, 29. Fairly common. In flower.

Utilization: The leaves may be boiled and eaten; they are rich in vitamin C and pro-vitamin A. The starchy root is edible raw but is usually boiled.

PORTULACACEAE (Purslane family)

1 genus; 2 species

Claytonia chamissoi Eschsch., toadlily. Habitat: wet slope. Elev. 20 ft. North prong of Kukak Bay. No. 523. August 5. In flower.

Claytonia scammaniana Hult. (?), Scamman springbeauty. Cozy Lakes, 58°13' N., 155°58' W. Muller 1261. July 15. "Not common" (Muller).

CARYOPHYLLACEAE (Pink family)

7 genera; 8 species

Stellaria crispa Cham. & Schlecht., crisp starwort. Habitat: moist rock bluff. Elev. 2,500 ft. Upper Knife Creek at east base of Knife Peak. Nos. 820, 821. August 7.

Stellaria longifolia Muhl., long-leaved starwort. Habitats: wet grass-willow flat; grass-willow bog. Elev. 120 ft. Lower American Creek; north shore of Lake Coville. Nos. 822, 823. July 7, 18. In flower.

Cerastium caespitosum Gilib., larger mouse-ear chickweed. Habitat: moist rocky bluff. Elev. 2,500 ft. Upper Knife Creek at east base of Knife Peak. No. 824. August 7. In flower.

Sagina intermedia Fenzl, snow pearlwort. Habitat: dry ridge. Elev. 2,000-2,300 ft. Head of Knife Creek; head of Katmai River. Nos. 518, 817. June 29, July 28. Fruiting.

Honckenya peploides (L.) Ehrh., seabeach sandwort. Habitats: sandy shore; mud flat; beach dune. Elev. 30-100 ft. Kinak Bay; Kukak Bay; Hallo Bay. Nos. 521, 522, 679. July 11, 24, August 4. In flower and fruiting.

Arenaria arctica Steven, Arctic sandwort. Elev. 1,000-2,500 ft. Angle Creek, 58°13' N., 155°27' W.; Mount Katolinat. Muller 1192, 1218. July 11, 13. "Fairly common" (Muller). Specific identity of No. 1218 is not certain.

Moehringia lateriflora (L.) Fenzl, blunt-leaved sandwort. Habitats: willow-spruce-cottonwood woods; cottonwood grove. Elev. 50-250 ft. 6 miles northwest of Coville River; $\frac{1}{4}$ mile west of mouth of Brooks River. Nos. 818, 819. July 8, 26. In flower.

Silene acaulis L., moss campion. Elev. 1,500-2,500 ft. Northeast of Hidden Harbor; ridge between Kukak and Kaffia Bays. Nos. 519, 520. July 26, 27. Fruiting.

RANUNCULACEAE (Crowfoot family)

6 genera; 8 species

Caltha natans Pallas, floating marsh marigold. Habitat: mud flat. Elev. 110 ft. Mouth of American Creek. Nos. 801, 802, 803, 804, 805. July 18. In flower.

Delphinium glaucum Watson, larkspur. Habitat: grassy slope at cannery. Elev. 20 ft. Kukak Bay. Nos. 516, 517. August 3. In flower.

Aconitum delphinifolium DC., delphinium-leaved aconite. Habitat: cottonwood grove. Elev. 50-250 ft. 1 mile east of mouth of Brooks River; $\frac{1}{4}$ mile west of mouth of Brooks River; 1 mile north of mouth of Brooks River; Kuikpalik Island. Nos. 514, 515, 806, 807, Muller 1265. July 15, 17, 29, August 14. In flower. Fairly common.

Anemone narcissiflora L., narcissus-flowered anemone. Elev. 1,000-2,000 ft. Cozy Lakes, $58^{\circ}13' N.$, $155^{\circ}58' W.$ Muller 1239. July 16. "Fairly uncommon" (Muller).

A. narcissiflora var., narcissus-flowered anemone. Elev. 2,000 ft. Mount Dumpling. No. 513. July 10. Fruiting.

NOTE.—Subsp. *villosissima* DC. was collected July 1, 1899, at Kukak Bay by Coville and Kearney; subsp. *alaskana* Hult. was collected at the head of Naknek Lake, July 2, 1919, by Miller. Specimens are in the U. S. National Herbarium. (Hultén, 1944, pp. 732-733.)

Utilization: The early spring growth on upper end of root is edible; it has a waxy, mealy texture and taste.

Anemone richardsonii Hook., yellow anemone. Habitats: above timberline; damp swale. Mountain south of Kulik Lake; south side of Coville Lake. Raup 331, 452. June 27, July 14.

Ranunculus hyperboreus Rottb., Arctic buttercup. Habitats: marshy slough; mud flat. Elev. 50 ft. $\frac{1}{4}$ mile east of mouth of Brooks River; mouth of American Creek. Nos. 797, 798. July 18, August 19.

Ranunculus trichophyllus Chaix, white water-crowfoot. Habitats: stream, near bank; river bottom, depth of water 4 to 5 ft.; small creek; mud flat at stream outlet. Elev. 60-250 ft. Lower American Creek; Coville River; Savanoski Village site; north shore of Lake Coville. Nos. 512, 793, 794, 795, 796. July 7, 16, 17, 18. In flower.

Thalictrum sparsiflorum Turcz., few-flowered meadowrue. Habitat: cottonwood grove. Elev. 200 ft. North shore of Grosvenor Lake. Nos. 799, 800. July 5. In flower.

PAPAVERACEAE (Poppy family)

1 genus; 1 species

Papaver radicatum Rottb. subsp. *alaskanum* (Hult.) J. P. Anderson, Arctic poppy. Habitats: moist, rocky bluff; dry ridge; pumice.

Elev. 1,000-3,000 ft. Head of Knife Creek, 200 ft. from Fourth Glacier of Knife Creek Glaciers; Knife Creek at east base of Knife Peak; upper Katmai Canyon; Cozy Lakes, $58^{\circ}13'$ N., $155^{\circ}58'$ W. Nos. 511, 808, 809, Muller 1162, 1260. June 29, July 8, 16, 28, August 7. "Uncommon" to "fairly common" (Muller); in flower, July 28; fruiting, June 29, August 7.

CRUCIFERAE (Mustard family)

6 genera; 6 species

Barbarea orthoceras Ledeb., winter cress. Habitats: cottonwood grove; wet willow-grass flat. Elev. 200-250 ft. Northwest shore of Grosvenor Lake; north shore of Lake Coville. Nos. 866, 867. July 5. In flower. An introduction from Asia.

Rorippa islandica (Oeder ex Murr.) Borbás var. *occidentalis* (Wats.) Butters & Abbe, marsh yellow cress. Habitats: marshy slough; gravel beach; mud flat beside stream. Elev. 20-200 ft. Kukak Bay; $\frac{1}{4}$ mile east of mouth of Brooks River; south shore, North Arm of Naknek Lake. Nos. 509, 510, 861, 862, 863, 864. August 3, 15, 19. In flower and fruit.

Cardamine bellidifolia L., alpine cress. Habitat: moist rock bluff. Elev. 500-2,400 ft. Upper Knife Creek, east base of Knife Peak; Cozy Lakes, $58^{\circ}13'$ N., $155^{\circ}58'$ W. Nos. 865, Muller 1263. July 17, August 5. Fruiting. Introduced from countries around the Mediterranean.

Draba borealis DC. Habitat: rock cliff, south side of island. Elev. 250 ft. Lake Coville, 2 miles northwest of Coville River. Nos. 852, 853, 854. July 8. Fruiting.

Arabis lyrata L. subsp. *occidentalis* (Wats.) Piper, Kamchatka rock cress. Habitats: stream margins; beaches; rocky bluffs; spruce-alder woods. Elev. 100-1,000 ft. Numerous localities. Nos. 508, 852, 853, 854, 855, 856, 857, 858, 859, 860, Muller 1177. 7 dates, July 7-August 15. In flower; fruiting.

Utilization: The leaves are edible either green or cooked.

Erysimum cheiranthoides L., wormseed mustard. Habitats: cottonwood grove; rocky island. Elev. 150 ft. Lake Coville, 2 miles north-

west of Coville River ; northwest shore of Grosvenor Lake ; islet north of Research Bay, Iliuk Arm. Nos. 506, 507, 868, 869. July 5, 8, 16. In flower.

CRASSULACEAE (Orpine family)

1 genus ; 1 species

Sedum roseum (L.) Scop. (var.?), roseroot. Habitat: "tundra." Elev. 2,000 ft. 2 miles north of Idavain Lake. Nos. 856, 857. August 29. Fruiting.

S. roseum subsp. *integrifolium* (Raf.) Hult., roseroot. Habitats: "tundra"; swales ; ridges ; rocky cliffs ; cottonwood groves. Elev. 100-2,500 ft. Numerous localities. Nos. 498, 499, 500, 501, 502, 503, 504, 505, 858, 859, 860, 861, Raup 333, Muller 1180, 1216. 11 dates, June 27-August 17. In flower, July 5-23 and August 17; fruiting, July 25, 29. Fairly common.

Utilization: The fleshy stems and leaves are edible either green or cooked. The root also may be eaten.

SAXIFRAGACEAE (Saxifrage family)

4 genera ; 10 species

Saxifraga bronchialis L. subsp. *funstonii* (Small) Hult., spotted saxifrage. Habitat: rocky places. Elev. 200-2,500 ft. Northwest shore of Grosvenor Lake ; Lake Coville, 2 miles northwest of Coville River ; Angle Creek (two localities, 58°13' N., 155°24' W. and 27' W.). Nos. 862, 863, Muller 1173, 1187. July 5, 8, 10, 11. In flower. "Common" and "not abundant" in two localities on Angle Creek (Muller).

Saxifraga ferruginea Graham, Alaska saxifrage. Elev. 1,000-2,000 ft. Angle Creek, 58°13' N., 155°27' W. Muller 1185. July 11. "Not common" (Muller).

Saxifraga flagellaris Willd., flagellate saxifrage. Habitat: steep-faced bedrock wall. Elev. 2,000-3,000 ft. Cozy Lakes, 58°13' N., 155°58' W.; Angle Creek, 58°13' N., 155°27' W. July 11, 16. Muller 1179, 1258. "Rather uncommon" at Cozy Lakes (Muller).

Saxifraga hieracifolia Waldst. & Kit., hawkweed-leaved saxifrage. Elev. 600 ft. Cozy Lakes, 58°13' N., 155°58' W. Muller 1249. July 16. "Not common" (Muller).

Saxifraga punctata L., brook saxifrage. Elev. 1,000-2,300 ft. Upper Katmai Canyon; head of Katmai River. Nos. 488, 489. July 28. In flower; fruiting.

Utilization: The young leaves are palatable (raw) and a good source of vitamin C and pro-vitamin A.

S. punctata subsp. *insularis* Hult., brook saxifrage. Habitat: near streamlets. Angle Creek, 58°13' N., 155°24' W.; Cozy Lakes, 58°13' N., 155°58' W. Muller 1174, 1243, 1254. July 10, 16, 17. "Not uncommon" (Muller).

S. punctata subsp. *nelsoniana* (D. Don) Hult., brook saxifrage. Habitat: moist rock bluff. Elev. 2,400 ft. Upper Knife Creek, east base of Knife Peak. Nos. 864 (sterile), 865, 866, 867 (in flower and fruit). August 7.

S. punctata subsp. *pacifica* Hult., brook saxifrage. Angle Creek, 58°13' N., 155°24' W. Muller 1197. July 11.

Saxifraga serpyllifolia Pursh, thyme-leaved saxifrage. Elev. 1,700-3,000 ft. Cozy Lakes, 58°13' N., 158°58' W. Muller 1242, 1262. July 16, 17. "Common" and "uncommon" in two places (Muller).

Heuchera glabra Willd., alpine heuchera. Habitats: rocky bluffs and ridges; cottonwood grove. Elev. 20-2,500 ft. Numerous localities. Nos. 490, 491, 492, 493, 494, 495, 496, 872, 873, 874, 875, Muller 1182, 1214, 1235. 10 dates July 11-August 17. In flower, July 11-August 17. Locally common.

Parnassia palustris L., northern grass-of-Parnassus. Habitats: birch-willow-cottonwoods; cottonwood grove; streamsides. Elev. 50-250 ft. South shore of Grosvenor Lake, 7 miles east of Coville River; $\frac{1}{4}$ mile west of mouth of Brooks River; Savanoski Village site; northwest shore of Iliuk Arm. Nos. 497, 868, 869, 870, 871, Muller 1202. July 12, 17, 22, August 14, September 1. In flower. "Common" (Muller).

Ribes lacustre (Pers.) Poir., swamp gooseberry. Habitat: rock bluff at side of lake. Elev. 200 ft. South shore of Grosvenor Lake, 10 miles east of Coville River. No. 876. July 22. Fruiting.

Ribes triste Pall., American red currant. Habitats: mixed woodland; cottonwood grove. Elev. 50-250 ft. Northwest shore of Grosvenor Lake; 6 miles northwest of Coville River; northwest shore of Iliuk Arm. Nos. 877, 878, 879, 880, 881, 882, 883. July 5, 8, September 1. Fruiting (few and overmature berries, September 1).

ROSACEAE (Rose family)

7 genera; 18 species

Spiraea beauverdiana Schneider, Beauverd spirea. Habitats: ridges; lake margin; mixed woods; wet grass-willow flat. Elev. sea level-2,000 ft. Numerous localities. Nos. 478, 479, 480, 481, 482, 483, 484, 701, 702, 703, 704, 705, 706, 707, 708, Muller 1178. 9 dates, July 5-Sept. 6. In flower, July 5-24; fruiting, July 25-September 6. A common and widespread plant.

Luetkea pectinata (Pursh) Kuntze, luetkea. Habitats: dry ridges; tundra. Elev. 50-2,700 ft. Numerous localities. Nos. 485, 486, 487, 695, Muller 1211, 1244. 6 dates, July 10-August 2. In flower, July 10-August 2; fruiting, July 24, 26. "Abundant" (Muller).

Rubus chamaemorus L., cloudberry. Habitats: ridge; cottonwood grove; damp tundra below old terrace. Elev. 50-500 ft. South shore of Naknek Lake at west boundary of Monument; $\frac{1}{4}$ mile west of mouth of Brooks River; south side of Idavain Lake. Nos. 699, 700, Raup 339. June 27, August 14, 17. Fruiting.

Utilization: The berry is a very rich source of vitamin C, containing several times as much of the antiscorbutic material as fresh orange. The vitamin is retained if the berries are frozen immediately after picking—otherwise it is soon lost.

Rubus spectabilis Pursh, salmonberry. Habitat: grass-alder peninsula. Elev. 50 ft. Kafia Bay. Nos. 696, 697. July 11. In flower.

Utilization: An easily gathered fruit during August; fairly palatable although insipid when compared with cloudberry and raspberry.

Rubus stellatus J. E. Sm., nagoonberry. Habitats: cottonwood grove; bluff; wet swale. Elev. 100-2,000 ft. Alagogshak Creek; Mount Dumpling; Kuikpalik Island; northwest shore of Grosvenor Lake. Nos. 463, 464, 465, 466, 467, 468, 698. July 5, 10, 28, 29. In flower.

Utilization: The fruit is excellent for immediate consumption or as jelly, but is nowhere abundant.

Potentilla fruticosa L., shrubby cinquefoil. Elev. 2,000 ft. 3 miles north of west end of Grosvenor Lake. No. 453. August 17. Fruiting.

Potentilla hookeriana Lehm. (?), Hooker cinquefoil. Elev. 2,000 ft. 3 miles north of west end of Grosvenor Lake. No. 449. August 17. Fruiting.

Potentilla monspeliensis L., rough cinquefoil. Habitat: rocky islands. Elev. 40-250 ft. Lake Coville, 2 miles northwest of Coville River; rocky island north of Research Bay, Iliuk Arm. Nos. 451, 452, 689. July 8, 16. In flower.

Potentilla nivea L. (?), snow cinquefoil. Habitat: very dry moraine. Elev. 500 ft. West end of Idavain Lake. Raup 337. June 27.

Potentilla palustris (L.) Scop., marsh cinquefoil. Habitats: grassy areas; mixed grass-willow or alder thickets; bluff. Elev. 50-250 ft. Alagogshak Creek; Hallo Bay; Brooks River; lower American Creek; 3 miles southwest of Lake Coville. Nos. 454, 455, 456, 457, 690, 691, 692. July 11, 18, 25, August 14, 17. In flower.

Potentilla villosa Pall., villous cinquefoil. Habitat: rock bluffs and broken rocks. Elev. 50-200 ft. Kuliak Bay; northwest shore of Grosvenor Lake; Katmai River. Nos. 450, 687, 688. July 5, 11, 25. In flower, July 5, 11; fruiting, July 25.

Potentilla virgulata A. Nels., cinquefoil. Habitat: rock cliff, south side of island. Elev. 250 ft. Lake Coville, 2 miles northwest of Coville River. Nos. 693, 694. July 8. In flower.

Potentilla (sp. ?), cinquefoil. Elev. just above sea level. Swikshak Lagoon. No. 448. August 4. In flower.

Geum calthifolium Menzies, caltha-leaved avens. Elev. 100-1,500 ft. Ridge between Kukak and Kafia Bays; Cape Douglas. Nos. 458, 459, 460. July 27, 29. In flower, July 27; fruiting, July 29.

Geum macrophyllum Willd., large-leaved avens. Habitats: cottonwood grove; grass-alder woods. Elev. 30-200 ft. Northwest shore

of Grosvenor Lake; Kaslia Bay. Nos. 682, 683, 684, 685, 686. In flower.

Geum rossii (R. Br.) Ser., Ross avens. Mount Katolinat. Muller 1217. July 13. "Not common" (Muller).

Dryas octopetala L. subsp. *punctata* (Juz.) Hult., eight-petaled mountain avens. Habitat: ridgetop. Elev. 2,500 ft. 5 miles north-west of Kaguyak Crater. Nos. 461, 462. July 23.

Sanguisorba menziesii Rydb., Menzies great burnet. Elev. 2,000 ft. 3 miles north of west end of Grosvenor Lake. No. 470. August 17. In flower.

Sanguisorba sitchensis C. A. Meyer, Sitka great burnet. Habitats: tundra; grassy areas; damp woods. Elev. 50-2,000 ft. Numerous localities. Nos. 469, 471, 473, 474, 475, 476, 477, 709, 710, 711, 712, 713, Muller 1201, 1248. 11 dates, July 11-August 29. In flower. A widespread and fairly common species.

LEGUMINOSAE (Pulse family)

4 genera; 6 species

Lupinus nootkatensis Donn, Nootka lupine. Habitats: grassy areas; beach dune; fairly dry tundra. Elev. 30-700 ft. Hallo Bay; Alagoshak Creek; west end of Idavain Lake; Takli Island, Amalik Bay; Katmai River; Kuikpalik Island. Nos. 439, 440, 441, 442, 443, 445, 678, Raup 332. June 27, July 11, 25, 29. In flower.

Utilization: The roots are eaten by the Aleuts, either raw or cooked, after being carefully scraped to remove the skin. However, excessive amounts are believed to produce fatal inflammation of the stomach and intestines.

L. nootkatensis var.?, Nootka lupine. Habitat: ridge. Elev. 50 ft. South shore of Naknek Lake at west boundary of Monument. Nos. 680, 681. August 17. In flower.

Astragalus alpinus L. subsp. *alaskanus* Hult., alpine milk vetch. Habitat: streamside in cottonwood grove. Elev. 150 ft. North shore of Grosvenor Lake, 5 miles east of Coville River. Nos. 714, 715. July 12. In flower.

Oxytropis gracilis (A. Nels.) K. Schum., northern yellow oxytrope. Habitat: "tundra." Elev. 2,000 ft. Mount Dumphling. No. 682. August 2. In flower.

Oxytropis nigrescens (Pall.) Fisch., blackish oxytrope. Elev. 2,300 ft. Head of Katmai River. Nos. 446, 447. July 28. Fruiting.

Oxytropis (sp.?), oxytrope. Habitat: gravel ridge. Elev. 2,100 ft. Junction of north and south forks of Knife Creek. No. 894. August 7.

Utilization: Several species of this genus are toxic. The root of *O. nigrescens* is eaten by the Eskimos of Barter Island. If used in emergencies, it should be taken in small amounts.

Lathyrus maritimus (L.) Bigel., beach pea. Habitats: beaches on lakes, rivers, and coastal bays. Elev. 30-250 ft. Hallo Bay; north shore of Lake Coville, 6 miles northwest of Coville River; mouth of Margot Creek, Iliuk Arm; Iliuk Moraine, south of Iliuk Arm. Nos. 436, 675, 676, 677, Muller 1233. July 8, 11, 13, 16. In flower.

Lathyrus palustris L., wild pea. Habitats: willow-alder woods; streamside in willows. Elev. sea level-250 ft. 1 mile west of mouth of Brooks River; 1 mile east of mouth of Brooks River; south shore of Grosvenor Lake, 7 miles east of Coville River; Swikshak Lagoon. Nos. 437, 438, 672, 673, 674. July 15, 22, 26, August 4. In flower.

L. palustris subsp. *pilosus* (Cham.) Hult., wild pea. Habitat: cottonwood grove. Elev. 200 ft. Northwest shore of Grosvenor Lake. No. 716. July 5. In flower.

GERANIACEAE (Geranium family)

1 genus; 1 species

Geranium cريانثum DC., northern geranium. Habitats: grassy flats; grass-alders; willow-alder woods; "tundra"; moist rock bluff. Elev. 30-2,000 ft. Numerous localities. Nos. 432, 433, 434, 435, 665, 666, 667, 668, 669, 670, 671, Muller 1237. 8 dates, July 5-29. In flower throughout July; fruiting, July 24. A common plant in many areas.

EMPETRACEAE (Crowberry family)

1 genus; 1 species

Empetrum nigrum L., crowberry. Habitats: "tundra"; birch-willow hills and ridges. Elev. 20-2,000 ft. Numerous localities. Nos. 139, 140, 141, 142, 143, 144, 145, 660, 661, 662, 663, 664. 5 dates, July 10-August 17.

Utilization: Although the raw berries are mealy and tasteless, they are more flavorful when cooked. They are good as pie and jelly. The natives mix the raw berries with other fruit, especially blueberries.

VIOLACEAE (Violet family)

1 genus; 2 species

Viola glabella Nutt. (?), stream violet. Elev. 100-130 ft. Cape Douglas; Kuikpalik Island. Nos. 137, 138. July 29.

Viola langsдорfi Fisch., Alaska violet. Habitat: swale. Elev. 700 ft. South side of Idavain Lake. Raup 335. June 27.

ONAGRACEAE (Evening-primrose family)

1 genus; 7 species

Epilobium adenocaulon Hausskn., northern willowherb. Habitat: stream bank. Elev. 150 ft. Brooks River. Nos. 654, 655, 656. August 23. Fruiting.

Epilobium angustifolium L., fireweed. Habitat: grassy swales, moist and dry. Elev. 20-2,000 ft. Numerous localities. Nos. 110, 111, 112, 122, 123, 124, 125, 126, 135, 136. 10 dates, July 10-August 3. In flower, July 15-August 3.

Utilization: The young plants are edible as a pot herb; they are a good source of vitamin C and pro-vitamin A. The following form is equally useful in this respect.

E. angustifolium forma *spectabile* (Simmons) Fern., fireweed. Habitat: grassy openings in alder woods. Elev. 20 ft. Kukak Bay. Nos. 113, 114, 115, 116. August 3. In flower.

Epilobium glandulosum Lehm., glandular willowherb. Elev. 20 ft. Kukak Bay. Nos. 108, 109. August 3. Fruiting.

Epilobium hornemannii Rchb., Hornemann willowherb. Habitats: wet swale; moist rock bluff. Elev. 2,000-2,400 ft. Angle Creek, $58^{\circ}13'$ N., $155^{\circ}24'$ W.; upper Knife Creek, east base of Knife Peak; Mount Dumphling. Nos. 106, 107, 652, 653, 893, Muller 1196. July 10, 11, August 7. In flower, July 10, August 7; fruiting, August 7. Identity of Collection No. 106 cannot be determined with certainty.

Epilobium latifolium L., dwarf fireweed. (Pl. 6, fig. 1.) Habitats: widespread; open and grassy areas. Elev. 50-2,400 ft. Numerous localities. Nos. 102, 103, 104, 117, 118, 119, 120, 121, 127, 128, 129, 130, 131, 132, 133 (in flower), 134, 657, 658, 659, Muller 1154. 11 dates, July 5-August 17. In flower, July 5-August 28; fruiting, July 17-August 28.

Utilization: The young shoots are edible as greens, especially when mixed with other species.

E. latifolium is a pioneer plant that stabilizes raw pumice slopes. It is one of the most conspicuous species on gravel ridges and pumice flats in upper Knife Creek; a pioneer in revegetating the devastated area.

Epilobium leptocarpum Hausskn., thin-capsuled willowherb. Habitat: streamside. Elev. 2,000 ft. Angle Creek, $58^{\circ}13'$ N., $155^{\circ}27'$ W. Muller 1186. July 11. "Common" (Muller).

Epilobium palustre L., swamp willowherb. Habitat: marsh. Elev. 100 ft. 1 mile north of mouth of Brooks River. No. 105. July 13. Fruiting.

HIPPURIDACEAE (Marestalk family)

1 genus; 1 species

Hippuris vulgaris L., common marestalk. Habitats: stream margin; marshy slough. Elev. 60-220 ft. Savanoski; mouth of Ukak River; $\frac{1}{4}$ mile east of mouth of Brooks River. Nos. 649, 650, 651. June 30, August 2, 19. Identity of No. 649 is not certain, but probably is this species.

Utilization: The Eskimos use this species as soup by boiling it in water. Seal oil and sometimes fish eggs, tom-cod livers, or seal meat are cooked with it.

UMBELLIFERAE (Parsley family)

6 genera; 6 species

Bupleurum americanum Coult. and Rose, American thoroughwort. Habitat: "tundra." Elev. 250-2,000 ft. Mount Dumpling; Iliuk Moraine, south of Iliuk Arm, 58°26' N., 155°38' W. Nos. 646, Muller 1230. July 13, August 2. In flower.

Cicuta mackenziana Raup, Mackenzie water hemlock. Habitat: grassy flat. Elev. 30 ft. Hallo Bay. Nos. 101, 595. July 11, August 4. In flower.

Utilization: All parts of the plant, but especially the root, contain a resinlike, toxic substance called cicutoxin. A small quantity of the root is sufficient to cause death.

Ligusticum hulténii Fern., Hultén sea lovage. Habitat: grassy flat. Elev. 30 ft. Hallo Bay. No. 582. July 11. In flower.

Conioselinum benthamii (Wats.) Fern., western hemlockparsley. Habitats: dry and moist rock cliffs; grassy areas. Elev. 50-500 ft. Numerous localities. Nos. 95, 96, 97, 98. 99, 646, 647, 648. July 8, 24, 25, 29, August 15. In flower.

Angelica lucida L., seacoast angelica. (Pl. 6, fig. 2.) Habitat: grassy areas. Elev. 100-1,500 ft. Numerous localities. Nos. 86, 87, 88, 89, 90, 91, 92, 93, 94. 7 dates, July 23-August 3. In flower.

Utilization: The young stems and leafstalks may be peeled and eaten raw; they have a strong celerylike flavor. The leaves are edible when cooked, or boiled with fish.

Heracleum lanatum Michx., cow parsnip. Habitat: wet swale in tundra. Elev. 2,000 ft. No. 100. Mount Dumpling. July 11. Fruiting.

Utilization: A pot herb. The inner pulp of young stems and leaf stalks is edible in the raw state. The root, when cooked, is said to taste like rutabaga.

CORNACEAE (Dogwood family)

1 genus; 1 species

Cornus suecica L., Lapland cornel. Habitats: grassy swale; "tundra"; stony ridge; grass-alder-spruce. Elev. 50-2,000 ft. Nu-

merous localities. Nos. 84, 85, 642, 643, 644, 645, Raup 334. June 27, July 11, 29, September 6. In flower, July 11; fruiting, July 29-September 6. Abundant.

PYROLACEAE (Wintergreen family)

2 genera; 2 species

Moneses uniflora (L.) A. Gray, single delight. Habitat: poplar-willow-alder-birch woodland near river. Elev. 20-250 ft. Iliuk Moraine, south of Iliuk Arm, 58°26' N., 155°38' W.; Hallo Bay. Nos. 70, Muller 1229. July 13, August 4. In flower. "Fairly common" south of Iliuk Arm (Muller).

Pyrola asarifolia Michx., liver-leaf wintergreen. Habitat: stream-side in cottonwood grove. Elev. 150 ft. North shore of Grosvenor Lake, 5 miles east of Coville River. No. 639. July 12. In flower.

P. asarifolia var. *incarnata* (Fisch.) Fern., liver-leaf wintergreen. Habitat: willow-alder woods. Elev. 50-250 ft. 1 mile west of mouth of Brooks River; 1 mile east of mouth of Brooks River. Nos. 69, 640, 641. July 15, 26. Fruiting.

ERICACEAE (Heath family)

6 genera; 8 species

Ledum palustre L. subsp. *decumbens* (Ait.) Hult., narrow-leaved Labrador tea. Habitats: dry tundra on old lake terrace; wet grass-willow flat; tundra near birch-cottonwood scrub; ridges. Elev. 500 ft. Numerous localities. Nos. 76, 77, 78, 79, 632, 633, 634, Raup 348. June 27, 30, July 7, 24, August 17, September 6. In flower, June 30, July 7; fruiting, August 17, 24. Abundant.

Utilization: The leaves make a palatable tea, but in too large amounts it may be cathartic.

Rhododendron camtschaticum Pall., Kamchatka rhododendron. Habitats: dry tundra; wet swale in tundra; sandy ridge; rocky islands. Elev. 50-2,500 ft. Kinak Bay; crest of Mount Dumpling; ridge between Kukak and Kafilia Bays; 3 miles north of west end of Grosvenor Lake; Mount Katolinat. Nos. 71, 72, 73, 74, 75, Muller 1212. July 10, 13, 24, 25, August 17. In flower, July 10, 25; fruiting,

July 24, August 17. Widespread and fairly common on suitable soils, but not abundant.

The specimens in Collection No. 71 may represent a variety.

Loiseleuria procumbens (L.) Desv., alpine azalea. Habitat: dry tundra on old terrace. Elev. 500-2,000 ft. Crest of Mount Dumping; ridge between Kukak and Kafia Bays; south side of Idavain Lake. Nos. 80, 81, 82, Raup 344. June 27, July 10, 25. Fruiting, July 10, 25.

Andromeda polifolia L., bog rosemary. Habitat: damp tundra. Elev. 700 ft. Idavain Lake. Raup 342. June 27.

Arctostaphylos alpina (L.) Spreng., alpine bearberry. Elev. 100 ft. Cape Douglas. No. 69. July 29.

Utilization: The berries are edible but usually too scattered to be worth gathering. They are insipid when raw but much more flavorful when cooked.

Vaccinium ovalifolium Smith, bilberry. Elev. 50 ft. Hallo Bay. No. 360. August 4.

Utilization: The berries are edible either raw or cooked; they are a fair source of vitamin C.

Vaccinium uliginosum L., bog blueberry. Habitats: dry, stony ridges; damp tundra. Elev. 100-2,000 ft. Numerous localities. Nos. 65, 66, 67, 635, 636, 637, Raup 343. 6 dates, June 27-September 6.

Utilization: The berries are edible either raw or cooked. They are a fair source of vitamin C.

Vaccinium vitis-idaea L., mountain cranberry. Habitats: tundra; dry flats and ridges. Elev. 100-200 ft. 2 miles east of Naknek; 5 miles northwest of Kaguyak. Nos. 68, 638. June 30, July 24. In flower, June 30.

Utilization: The berries are good as sauce and jelly; they can be stored under water without cooking. In the raw stage, the berries are acid.

DIAPENSIACEAE (Diapensia family)

1 genus; 1 species

Diapensia lapponica L. subsp. *obovata* (Fr. Schmidt) Hult., diapensia. Elev. 2,000 ft. 3 miles north of west end of Grosvenor Lake. No. 83. August 17.

PRIMULACEAE (Primrose family)

3 genera; 3 species

Androsace septentrionalis L. Habitat: rock cliff, south side of island. Elev. 250 ft. Lake Coville, 1 mile northwest of Coville River. No. 625. July 8. Fruiting.

Dodecatheon radicans Greene, American cowslip. Habitat: grass-alder-spruce peninsula. Elev. 50 ft. Kuliak Bay. Nos. 622, 623, 624. July 11. In flower.

Trientalis europaea L., starflower. Habitats: grassy areas; willow-alder woods; cottonwood grove. Elev. 30-200 ft. Hallo Bay; west end of Grosvenor Lake; northwest shore of Grosvenor Lake; 1 mile west of mouth of Brooks River; Kafia Bay. Nos. 626, 627, 628, 629, 630, 631. July 5, 11, 26. In flower, July 5-11; early fruiting stage, July 26.

T. europaea subsp. *arctica* (Fisch.) Hult., starflower. Habitat: wet swale. Elev. 2,000 ft. Mount Dumpling. No. 146. July 11. In flower. The plant is recorded from Kukak Bay, 1899, Coville and Kearney; and from Katmai Bay, 1917, Hagelbarger (Hultén, 1948, p. 1292).

GENTIANACEAE (Gentian family)

3 genera; 4 species

Gentiana algida Pall., whitish gentian. Cozy Lakes, 58°13' N., 155°58' W. Muller 1250. July 15. "Not common, but widespread" (Muller).

Gentiana propinqua Richards., four-parted gentian. Elev. 2,000 ft. Crest of Mount Dumpling. No. 355. July 10. In flower.

Swertia perennis L. Elev. 100 ft. Tundra. Cape Douglas. Nos. 356, 357. July 29. In flower.

Menyanthes trifoliata L., buckbean. Habitats: stream margin; marsh. Elev. 40-300 ft. Mouth of Ukak River; 1 mile north of mouth of Brooks River. Nos. 358, 359, 621. July 13, August 2. In flower, July 13; fruiting, August 2.

Utilization: It is possible to use the rootstocks as a breadflour by drying and grinding them; the meal is then washed in several changes of water to leach out the bitter property.

POLEMONIACEAE (Polemonium family)

1 genus; 4 species

Polemonium acutiflorum Willd., Greek valerian. Habitat: bog. Elev. 40-150 ft. 3 miles southwest of Lake Coville; unnamed island north of Research Bay, near the south shore of Iliuk Arm. Nos. 349, 350. July 16, August 17. In flower.

Polemonium boreale Adams, northern Greek valerian. Elev. 4,500 ft. 2 miles south of Kukak Volcano. No. 354. July 26. In flower.

Polemonium coeruleum L. var. *villosum* (Rud.) Brand, Jacob's ladder. Habitats: willow-grass flats; cottonwood grove. Elev. 100 ft. North shore of Lake Coville; Brooks River; $\frac{1}{4}$ mile west of mouth of Brooks River. Nos. 616, 617, 618, 619, 620. July 7, August 14. In flower.

This species, or *P. acutiflorum*, has been recorded from Kukak Bay (Kincaid), Katmai Bay and Kashvik Bay (Hagelbarger), and Katmai Valley (July 28, 1915, Griggs) (Hultén, 1948, pp. 1321-1322).

Polemonium pulcherrimum Hook., Greek valerian. Habitats: rock bluff; rocky island. Elev. 50-200 ft. Iliuk Moraine, south of Iliuk Arm; northwest shore of Grosvenor Lake; Katmai River. Nos. 351, 352, 353, 615, Muller 1232. July 5, 13, 25. In flower.

HYDROPHYLLACEAE (Waterleaf family)

1 genus; 1 species

Romanzoffia sitchensis Bong., mist maid. Habitat: moist rock bluff. Elev. 2,400 ft. Upper Knife Creek at east base of Knife Peak. Nos. 613, 614. August 7. In flower.

BORAGINACEAE (Borage family)

1 genus; 1 species

Mertensia maritima (L.) S. F. Gray, sea lungwort. Habitat: beach dune. Elev. 20 ft. Hallo Bay. Nos. 611, 612. July 11. In flower.

SCROPHULARIACEAE (Figwort family)

5 genera; 6 species

Mimulus guttatus DC., yellow monkeyflower. Habitats: stream margins; mud flat; cliff near waterfall. Elev. sea level-1,200 ft. North prong of Kukak Bay; mouth of American Creek; Savanoski Village site; Angle Creek, $58^{\circ}13'$ N., $155^{\circ}24'$ W. Nos. 341, 342, 343, 598, 599, 600, Muller 1198. In flower.

Veronica americana (Raf.) Schwein., American brooklime. Habitat: shallow water in small streams. Elev. 60 ft. Savanoski. Nos. 344, 345, 601, Muller 1203. June 30, July 12, 17. In flower and fruit. No. 1203, "12-14 inches high. Abundant in small streamlets" (Muller).

Lagotis glauca Gaertn. Habitat: tundra. Elev. 2,000 ft. Crest of Mount Dumpling; Mount Dumpling; 3 miles north of west end of Grosvenor Lake; Cozy Lakes, $58^{\circ}13'$ N., $155^{\circ}58'$ W. Nos. 346, 347, 348, 610, Muller 1255. July 10, 15, August 2, 17. In flower. "Not abundant, but widely distributed" (Muller).

Castilleja hycophila Pennell, paintedcup. Habitat: grassy areas. Elev. 130-500 ft. Kuikpalik Island; Takli Island, Amalik Bay; Geographic Harbor. Nos. 335, 336, 337, 338. July 24, 25, 29. In flower. The specific identity of Nos. 336, 337, and 338 is not determinable with certainty.

Castilleja miniata Dougl. Habitat: "tundra." Elev. 2,000 ft. Mount Dumpling. Nos. 884, 885. August 2. In flower.

Rhinanthus minor Ehrh. subsp. *groenlandicus* (Chab.) Neum., rattlebox. Habitats: tundra and grassy areas; willow thicket on stream margin. Elev. 100-250 ft. Cape Douglas; Kuikpalik Island; south shore of Grosvenor Lake, 7 miles east of Coville River. Nos. 339, 340, 341, 602, 603. July 22, 29. In flower.

PLANTAGINACEAE (Plantain family)

1 genus; 1 species

Plantago juncooides Lam., seaside plantain. Habitat: wet mud flat. Elev. sea level. Head of Kukak Bay. No. 334. August 4.

Utilization: Related species of this genus, when young and tender in early summer, are used raw or cooked in boiling water. *P. juncooides* probably is useful in like manner.

RUBIACEAE (Madder family)

1 genus; 3 species

Galium boreale L., northern bedstraw. Habitats: cottonwood grove; willow-alder woods; stream border; rock cliff near water. Elev. 50-250 ft. Numerous localities. Nos. 331, 332, 333, 605, 606, 607, 608, 609, Muller 1240. 7 dates, July 8-26. In flower, July 8-26. A common plant in damp lowland woods.

Galium trifidum L. subsp. *columbianum* (Rydb.) Hult., bedstraw. Elev. 20 ft. Kukak Bay. No. 330. August 3. Fruiting.

Galium triflorum Michx. (?), sweet-scented bedstraw. Habitat: cottonwood grove. Elev. 100 ft. $\frac{1}{4}$ mile west of mouth of Brooks River. No. 604. August 14.

CAPRIFOLIACEAE (Honeysuckle family)

3 genera; 3 species

Sambucus racemosa L. subsp. *pubens* (Michx.) House, redberried elder. Habitats: grassy areas; woods borders; base of lava flow. Elev. 20-2,000 ft. Hallo Bay; Kukak Bay; Angle Creek, 58°13' N., 155°24' W. Nos. 326, 327, Muller 1167. July 10, August 3, 4. Fruiting. Common in sheltered bays off Shelikof Strait, but uncommon in the interior of the Monument.

Utilization: The berries are commonly believed to be inedible and to cause digestive disturbances.

Viburnum edule (Michx.) Raf., mooseberry. (Pl. 7, fig. 1.) Habitat: spruce forest. Elev. 50 ft. 1 mile east of mouth of Brooks River; Hallo Bay. Nos. 328, 329. July 15, August 4. Fruiting.

Utilization: The berries are used for a tart jelly.

Linnaea borealis L. subsp. *americana* (Forbes) Hult., twinflower. Habitat: south slope, birch-willow thickets. Elev. 150 ft. East end of Lake Coville. No. 597. July 16. In flower.

VALERIANACEAE (Valerian family)

1 genus; 1 species

Valeriana capitata Pall., capitate valerian. Habitat: streamside in cottonwood grove. Elev. 150 ft. North shore of Grosvenor Lake, 5 miles east of Coville River. No. 596. July 12. In flower.

CAMPANULACEAE (Bluebell family)

1 genus; 3 species

Campanula lasiocarpa Cham., mountain harebell. Habitats: rocky slopes; grassy areas. Elev. about 1,000-2,500 ft. Head of Katmai River; 3 miles north of west end of Grosvenor Lake; Mount Katolinat; Angle Creek, 58°13' N., 155°24' W. and 27' W. Nos. 324, 325, Muller 1170, 1190, 1213. July 10, 11, 13, 28, August 17. In flower. Fairly common but local in distribution. The species is recorded from Kukak Bay (Coville and Kearney), and from "Katmai region" and Mount Dumpling (Hagelbarger) (Hultén, 1949, p. 1458).

Campanula latisepala Hult. var. *dubia* Hult., mountain harebell. Elev. 130 ft. Kuikpalik Island. No. 322. July 29. In flower.

C. latisepala x *rotundifolia*, harebell (hybrid). Elev. 100 ft. Cape Douglas. No. 323. July 29. In flower.

Campanula rotundifolia L., harebell. Habitat: ridges and rocky places. Elev. 50-500 ft. Takli Island, Amalik Bay; Katmai River; Geographic Harbor. Nos. 319, 320, 321. July 24, 25. In flower.

COMPOSITAE (Composite family)

12 genera; 23 species

Solidago lepida DC. Habitat: bluff. Elev. 50-100 ft. Takli Island, Amalik Bay; Alagogshak Creek. Nos. 297, 298, 299, 300, 301. July 25, 28. In flower.

Solidago multiradiata Ait., northern goldenrod. Habitat: grassy areas. Elev. 100-2,000 ft. Numerous localities. Nos. 289, 290, 291, 292, 295, 588, 589, 590, 591, Muller 1238. July 16, 17, 22, 29, August 17. In flower. A common and widespread species.

Collection Nos. 289 and 290 are not positively identifiable as belonging to this species.

S. multiradiata var. *arctica* (DC.) Fern., northern goldenrod. Elev. 1,500-2,000 ft. Crest of Mount Dumpling; ridge between Kukak and Kafia Bays. Nos. 293, 294, 296. July 11, 27. In flower.

Aster sibiricus L., Siberian aster. Habitats: dry river course; well-drained moraine knoll at edge of river, volcanic ash soil. Elev. 200 ft. North shore of Grosvenor Lake, 10 miles east of Coville River; Angle Creek, $58^{\circ}13' N.$, $155^{\circ}27' W.$ Nos. 592, Muller 1176. July 11, 24. In flower.

Aster subspicatus Nees. Habitat: marshy area. Elev. 600-650 ft. South Fork of Kamishak River; Cozy Lakes, $58^{\circ}13' N.$, $155^{\circ}58' W.$ Nos. 313, Muller 1246, 1253. July 16, September 3. In flower. "Not abundant" (Muller).

Erigeron peregrinus (Pursh) Greene, fleabane. Elev. 1,500-2,000 ft. Ridge between Kukak and Kafia Bays; crest of Mount Dumpling. Nos. 314, 315, 316. July 11, 26. In flower.

Antennaria alaskana Malte, everlasting. Habitat: tundra. Elev. 1,500-2,000 ft. Crest of Mount Dumpling; ridge between Kukak and Kafia Bays. Nos. 269, 270. July 11, 26. Fruiting. Collection No. 270 is not positively identifiable as this species.

Antennaria monocephala DC. Habitat: very dry moraine. Elev. 700 ft. West end of Idavain Lake. Raup 336. June 27.

Achillea borealis Bong., northern yarrow. Habitats: grassy areas; open alder thickets; willow-alder woods. Elev. 20-2,000 ft. Numerous localities. Nos. 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 390, 574, 575, 576, 577, 578, 579, Muller 1231. 13 dates, July 7-August 17. In flower. One of the most common and widespread species.

Matricaria matricarioides (Less.) Porter, pineapple-weed. Habitat: developed area (camp). Elev. 50 ft. Brooks River. No. 593. August 14. In flower. Introduced.

Chrysanthemum arcticum L., Arctic daisy. Habitats: grassy flats and dunes. Elev. 30-100 ft. Cape Douglas; Hallo Bay; Swikshak Lagoon. Nos. 316, 317, 318, 580. July 11, 29, August 4. In flower.

Artemisia arctica Less., Arctic wormwood. Habitat: tundra. Elev. 200-2,500 ft. 5 miles northwest of Kaguyak; Mount Dumpling; crest of Mount Dumpling; ridge between Kukak and Kafliia Bays; 5 miles northwest of Kukak Crater. Nos. 279, 280, 281, 282, 581. July 10, 23, 24, 27, August 2. In flower.

Artemisia globularia Cham. Elev. 1,500-2,000 ft. Cozy Lakes, 58°13' N., 155°58' W. Muller 1257. July 16. "Not uncommon" (Muller).

Artemisia tilesii Ledeb. Habitat: pumice. Elev. 1,000 ft. Upper Katmai Canyon. Nos. 283, 284, 285, 286. July 28. In flower.

A. tilesii subsp. *gormanii* (Rydb.) Hult. Habitats: tundra; seep in mud flow. Elev. 40-2,000 ft. Junction of Ukak and Savanoski Rivers; 3 miles north of west end of Grosvenor Lake. Nos. 287, 288. July 17, August 17. In flower.

Utilization: The fresh or dried leaves of a related plant are used as a poultice for eye conditions.

Petasites frigidus (L.) Fries, Arctic sweet coltsfoot. Habitat: cottonwood grove. Elev. 100 ft. $\frac{1}{4}$ mile west of mouth of Brooks River. No. 594. August 14.

Arnica chamissonis Less., arnica. Habitats: pumice; ridge. Elev. 500-2,300 ft. Kukak Bay; Geographic Harbor; head of Katmai River. Nos. 264, 265, 266. July 23, 24, 28. In flower.

Arnica lessingii Greene, arnica. Habitat: tundra. Elev. 2,000-2,500 ft. Mount Dumpling; crest of Mount Dumpling; 5 miles northwest of Kukak Crater. Nos. 267, 268, 587. July 10, 23, August 2. In flower.

Arnica louiscana Farr subsp. *frigida* (Meyer) Maguire. Elev. 1,500-2,700 ft. Mount Katolinat; Cozy Lakes, 58°13' N., 155°57' W. Muller 1219, 1256. July 13, 16. "Fairly common" (Muller).

Senecio congestus (R. Br.) DC., marsh fleabane. Habitat: wet seep in mud flow. Elev. 40 ft. Junction of Ukak and Savanoski Rivers. No. 274. July 17. In flower and fruiting.

S. congestus var. *palustris* (L.) Fern., marsh fleabane. Habitats: mud flat; stream margin. Elev. 40-110 ft. Mouth of American Creek; mouth of Ukak River. Nos. 583, 584, 585, 586. July 18, August 2. In flower.

Senecio lugens Richards., squaw-weed. Habitat: grassy area. Elev. 130 ft. Kuikpalik Island. Nos. 271, 272. July 29. Fruiting.

Senecio pseudo-arnica Less. Habitat: muddy flat. Elev. sea level. Head of Kukak Bay. No. 273. August 4. In flower.

Senecio resedifolius Less. Elev. 1,000-2,000 ft. Cozy Lakes, 58°13' N., 155°58' W. Muller 1241. July 16.

Senecio triangularis Hook. Elev. 1,000-2,000 ft. Cozy Lakes, 58°13' N., 155°58' W. Muller 1236. July 16. "Fairly common on slopes" (Muller).

Prenanthes alata (Hook.) Dietr., rattlesnake-root. Habitats: dry ridge; cliff near waterfall. Elev. 50-500 ft. Geographic Harbor; Cape Douglas; north prong of Kukak Bay. Nos. 275, 276, 277, 278. July 24, 29, August 5. In flower and fruiting.

Also known from Katmai Valley (July 28, 1915, Griggs) and Moose Creek (Hagelbarger, n.d.) (Hultén, 1950, p. 1666).

REVEGETATION FOLLOWING VOLCANISM

The effects of volcanic eruptions on vegetation have been studied in a number of areas. Griggs (1918, pp. 8-15) has summarized the results of observations at Krakatoa in Dutch East Indies, Taal in the Philippines, St. Vincent in the West Indies, Tarawera and the great pumice area of New Zealand, and the prehistoric eruption in the Upper Yukon Basin of Alaska. In the same series of papers (1918, 1919a, 1919b) Griggs reported on extensive investigations of the effects of the 1912 eruption on the vegetation of the region surrounding Mount Katmai and on nearby Kodiak Island. In part IX of the series Griggs (1919b) described "The Beginnings of Revegetation in Katmai Valley" as he found them in 1915, 1916, and 1917, three to five years after the eruption.

KATMAI VALLEY

Shielded as it was by the Aleutian Range, Katmai Valley did not experience the full violence of the 1912 eruption. Great damage was done by hot blasts and ash fall, but regeneration was well under way in a relatively short time. The botanists of the first three expeditions of the National Geographic Society found numerous instances of survival of woody plants. They also noted herbs that came up in spots from which pumice had been swept by wind, and seedlings that started in the ash deposits. Observation stations were established at points such as Katmai Village which could be relocated in future years, and records were made in writing and by photography.

It would have been desirable to record the plant life at these stations as it existed at the time of the Katmai Project, almost 40 years later. Circumstances (chiefly weather) prevented me from spending sufficient time in this region of the Monument. Nevertheless, some collections of specimens were obtained in Katmai Valley during the summer of 1953, and observations and photographs were made. The following compilation shows the plant species that I found at three collection stations in the drainage: A rock bluff in lower Katmai River, elevation 50 feet; a pumice-covered flat in upper Katmai Canyon, elevation 1,000 feet; and an east-facing slope near the head of Katmai River, elevation 2,000 feet. In the opposite column are listed the species that Griggs collected in 1915-1917, with notes made at that time concerning their relative abundance and progress toward recovery from the effects of the eruption. This information and the citations are from Griggs' contributions to the series "Scientific Results of the Katmai Expeditions of the National Geographic Society." The plant names in brackets are those that were used in the publication.

Plant Species of Katmai Valley

Cahalane, 1953	Griggs, 1915-1917
.....	<i>Gymnocarpium dryopteris</i> [<i>Dryopteris dryopteris</i> (L.) Christ.]. A few plants were found, 1916, on the south slope of Katmai Volcano (p. 189).
.....	<i>Athyrium filix-femina</i> subsp. <i>cylosorum</i> [<i>A. cylosorum</i> (Rupr.) C. Chr.]. In bog, 10 miles from Crater (p. 190); thrifty in Soluka River (= Creek) Valley (p. 193).
<i>Equisetum arvense</i> . Upper Katmai Canyon.	". . . was able to penetrate (ash) deposits that nothing else could come through" (p. 322); scarce in Soluka Valley (p. 193).

(Continued)

Plant Species of Katmai Valley—Continued

Cahalane, 1953

Griggs, 1915-1917

- Agrostis borealis*. Head of Katmai River.
- Calamagrostis canadensis*. Lower Katmai River; Upper Katmai Canyon.
Calamagrostis canadensis var. *scabra* [C. *langs-dorffi* (Link) Trin.] was "starting in many places as seedlings" (p. 329); on lowland below Katmai Crater (p. 189).
Deschampsia caespitosa (L.) Beauv. Seedlings were "starting in many places" (p. 329).
- Trisetum spicatum*. Head of Katmai River.
- Poa hispidula*. Head of Katmai River.
- Poa paucispicula*. Head of Katmai River.
- Poa pratensis*. Upper Katmai Canyon.
Elymus mollis [E. *arenarius* L.]. "Locally of great importance" near shore of Shelikof Strait (p. 322).
- Carex lyngbyei*. Lower Katmai River. A few plants of *Carex* sp. were found on the south slope of Katmai Volcano in 1916 (p. 189); base of Katmai Crater (p. 189).
- Carex macrochaeta*. Upper Katmai Canyon.
- Carex nesophila*. Head of Katmai River.
- Luzula parviflora*. Upper Katmai Canyon.
Salix alaxensis. "Almost completely recovered" (p. 187).
On south slope of Katmai Volcano, a few plants were found in 1916 (p. 189).
"... have in places almost completely recovered" (p. 320).
- Salix arctica*. Head of Katmai River.
Salix bebbiana. "Recovered to a considerable extent" (p. 187).
Salix glauca. A few plants were found, 1916, on south slope of Katmai Volcano (p. 189).
Salix sconleriana [S. *nuttallii* Cov.] "Recovered to considerable extent" (p. 187).
Betula kenaica. "New sprouts from roots were fairly abundant in Soluka Valley" (p. 187).
Betula nana subsp. *exilis* [B. *rotundifolia* Spach]. In bog, 10 miles from Crater (p. 190); also "thrifty" in Soluka Valley (p. 193).

(Continued)

Plant Species of Katmai Valley—Continued

Cahalane, 1953	Griggs, 1915-1917
<i>Alnus crispa</i> subsp. <i>sinuata</i> . Lower Katmai River.	In a considerable part of Katmai Valley "we saw only two or three small shoots" (p. 187); one seen alive in Soluka Valley (p. 193).
<i>Oxyria digyna</i> . Upper Katmai Canyon.	A few plants were found in 1916 on the south slope of Katmai Volcano (p. 189). <i>Cerastium</i> sp. A few plants were found, 1916, on the south slope of Katmai Volcano (p. 189).
<i>Sagina intermedia</i> . Head of Katmai River.
<i>Papaver radicum</i> . Upper Katmai Canyon. <i>Barbarea orthoceras</i> [<i>Campe barbarea</i> (L.) Wight] "Starting in many places" (p. 329). <i>Sedum roseum</i> subsp. <i>integrifolium</i> [<i>Rhodiola rosea</i> L.] A few plants in flower, 1916, on south slope of Katmai Volcano (p. 189).
<i>Saxifraga punctata</i> . Upper Katmai Canyon; head of Katmai River.
<i>Heuchera glabra</i> . Lower Katmai River.	A few plants were found in 1916, on the south slope of Katmai Volcano (p. 189). <i>Rubus spectabilis</i> . On lowland below Katmai Crater (p. 189).
<i>Potentilla villosa</i> . Lower Katmai River.	A few plants in flower, 1916, on the south slope of Katmai Volcano (p. 189). <i>Sanguisorba sitchensis</i> . On lowland below Katmai Crater (p. 189).
<i>Lupinus nootkatensis</i> . Lower Katmai River.	<i>Lupinus</i> sp. "In the more exposed places (in the valley-bottom) lupines are the only pioneers" (p. 325).
<i>Oxytropis nigrescens</i> . Head of Katmai River.	<i>Empetrum nigrum</i> . In bog, 10 miles from Crater (p. 190); also "thrifty" in Soluka Valley (p. 193).
<i>Epilobium angustifolium</i> . Upper Katmai Canyon.	<i>Epilobium alaskae</i> . "Starting in many places" (p. 329).
<i>Epilobium latifolium</i> . Head of Katmai River; Upper Katmai Canyon.
<i>Conioselinum benthamii</i> . Lower Katmai River. <i>Cornus succica</i> . In bog, 10 miles from Crater (p. 190); also "thrifty" in Soluka Valley (p. 193).

(Continued)

Plant Species of Katmai Valley—Concluded

Cahalane, 1953

Griggs, 1915-1917

.....	<i>Ledum palustre</i> subsp. <i>decumbens</i> [<i>L. decumbens</i> (Ait.) Lodd.]. In bog, 10 miles from Crater (p. 190).
.....	<i>Vaccinium uliginosum</i> . In bog, 10 miles from Crater (p. 190); also in Soluka Valley (p. 193).
.....	<i>Vaccinium vitis-idaea</i> [<i>Vitis-idaea vitis-idaea</i> (L.) Britton]. In bog, 10 miles from Crater (p. 190); also "thrifty" in Soluka Valley (p. 193).
.....	<i>Trientalis europaea</i> subsp. <i>arctica</i> [<i>T. arctica</i> (Ledeb.) Fisch.]. In bog, 10 miles from Crater (p. 190); also in Soluka Valley (p. 193).
<i>Polemonium pulcherrimum</i> . Lower Katmai River.	<i>Polemonium acutiflorum</i> . "Starting in many places" (p. 329).
<i>Campanula lasiocarpa</i> . Head of Katmai River.
<i>Campanula rotundifolia</i> . Lower Katmai River.
<i>Artemisia tilesii</i> . Upper Kat- mai Canyon.	Seedlings were starting in many of the more sheltered places (p. 329).
.....	<i>Artemisia tilesii</i> subsp. <i>gormanii</i> . "Starting in many places" (p. 329); on lowland below Katmai Crater (p. 189).
<i>Arnica chamissonis</i> . Head of Katmai River.

VALLEY OF TEN THOUSAND SMOKE

Unlike Katmai River valley, which was protected to a large extent by the Aleutian Range, the Valley of Ten Thousand Smokes took the full force of the eruption. In describing conditions as he found them during the summer of 1917, Griggs (1919a, p. 204) stated: "... all vestiges of life were consumed by fire. . . Throughout the upper portion of the Valley of Ten Thousand Smokes and its branches not a vestige of the vegetation which must once have covered it is to be found. So complete has been the destruction that no evidence of what happened to the plants remains to tell the tale. . . We could not reasonably suppose that the area had been devoid of all vegetation before the eruption. Indeed, we knew that there were once good-sized trees far up toward Katmai Pass. On the other hand, in the light of our acquaintance with conditions on the other side of the range, we were hesitant in hypothecating destructive agencies so intense as to eradicate the very evidence of their action."

In a popular account Griggs (1922, p. 209) briefly described the earliest stages in the return of vegetation to this valley: "Plants were practically absent in 1917. Not quite so, however, for around some of the mild vents moss and algae were beginning to start in places bathed by the warm breath of the fumarole."

Two years later the botanists found that "The most conspicuous change in the appearance of the Valley was due to . . . the beginning of an invasion of its hot soil by plant life. In the two years since 1917 the few minute beginnings of vegetation had increased until they formed in places conspicuous spots of bright green, visible sometimes for a mile.

"The new growth was composed of 'blue-green' algae and moss, which made a dense carpet around some of the fumaroles. The algae consisted of several genera that are common in hot springs; the moss was uniformly sterile." (Ibid., p. 223.)

On the National Geographic Society's sixth and last expedition to the Katmai region (1930) Griggs and his party found that an extremely interesting development had taken place. Considerable areas which had been bare 11 years earlier were covered with a dense mat of liverworts. These belonged to two species: *Cephalosiella byssacea* (Roth) Warnst., and *Isopaches bicrenatus* (Schmid.) Buch (as *Lophozia bicrenata*). "Their growth had become thick and heavy, the shoots densely felted together into continuous unbroken carpets half an inch thick." (Griggs, 1933, p. 103.) The botanists inferred that the development of the liverwort layer might have required the greater part of a decade, and that the layer had extended itself from the shelter of windbreaks nearly as far as the stability of the ground would permit. Mats of liverworts occurred on a number of mildly steaming areas in the Valley of Ten Thousand Smokes, where the ground presumably was pure ash. Griggs inferred that the liverworts were able to thrive on the nitrogen-free ash because they can survive on a low concentration of nitrogen compounds. He also believed that the accelerated development of the liverwort layer presaged rapid revegetation of the devastated area by higher plants.

In support of his belief that nitrogen was the critical factor in slowing the return of seed plants, Griggs mentioned the presence of ammonia in the emanations of fumaroles around Novarupta, and described vegetation conditions there in 1930: "Close to Novarupta volcano, in the very heart of the most completely devastated portion of the whole district—in an area which was buried to a great and unknown depth under incandescent ejecta—a number of isolated clumps

of grass, *Calamagrostis scabra* [= *C. canadensis* subsp. *langsдорffii*], have come up. These grasses are the more significant because, except for them and for mosses, liverworts, and algae around some of the fumaroles, there are no plant colonists whatever in the Valley of Ten Thousand Smokes, nor on the mountains which surround it. Outside this special area there is not a blade of grass for miles around." (Ibid., p. 101.)

This latter statement by Griggs, as well as his description of widespread and luxuriant growths of liverworts, are highly significant in view of conditions that obtained in 1953 and 1954. In the twenty-odd years since the last expedition of the National Geographic Society, plant life in the Valley of Ten Thousand Smokes had taken two marked and divergent courses. The lower forms had declined almost to the vanishing point, while the seed plants (as Griggs expected) had multiplied tremendously.

With the death of most of the fumaroles and widespread desiccation, algae and mosses had practically vanished from the welded tuff or "sand flow." Survivors (*Symploca muralis*, *Aspergillus sydowii*, *A. niger*, and *Penicillium purpurogenum*) still existed in the throats of fumaroles at the southeastern and southwestern base of Baked Mountain, and in the "hot" area about 1 mile north of Novarupta. These primitive plants could not persist, however, on the exposed surface of the ground where they had been plentiful at least until 1930. Warm steam no longer permeated the tuff, which was cold and dry. Rain falling on the tuff ran off at once. The result was the most sterile habitat imaginable.

The extensive mats of liverworts that Griggs found in 1930 had nearly or quite vanished by 1953-1954. I found no trace of them in walking many miles, covering the upper portion of the Valley of Ten Thousand Smokes from the River Lethe north to the foot of Knife Peak, and from the Knife Creek Glaciers to the westernmost ridges of Broken Mountain and Baked Mountain. It is possible that remnants of these tiny, inconspicuous plants were overlooked, but it is certain that the great colonies which formerly prevailed on the ash and to some extent on the welded tuff no longer existed.

If the tuff had become less favorable for plant life during the interval between 1930 and 1953-1954, the slopes and hills north of it were a much more populous habitat. A considerable number of species, ranging from horsetail (*Equisetum*) to fireweed (*Epilobium*) was found on the gravel-pumice ridges between Novarupta and the southeastern foot of Knife Peak, and west to the western base of

Baked Mountain. Willows (*Salix*) up to 30 inches tall were growing on the ridge between the main forks of upper Knife Creek and within a quarter of a mile of the snout of Number Four Glacier. Grasses and sedges (particularly *Calamagrostis canadensis*, *Poa arctica*, *P. hispidula*, and *Carex macrochaeta*) and alpine wood rush (*Luzula arcuata*) were present in some abundance, particularly along the bottoms of shallow depressions. (Pl. 11, fig. 1.) In these low places moisture collected during summer rains and as melting snow, but not in such amounts as to rush off immediately. Even here the plants survived only with great difficulty, for surface moisture tended to sink quickly through the very porous ground. Desiccation was a major hazard, and the plants growing on the ash had developed enormous root systems.

In addition to gathering sufficient water and food in the porous, sterile earth, the large roots also served to anchor the plants against another serious enemy—wind. Numerous willows showed evidence of sand-blasting by the violent williwaws that sweep the Valley in winter. Undoubtedly these winds, added to the effects of moderate cold, destroyed many twigs of the willows. Even the comparatively moderate winds of summer, which frequently reach velocities well exceeding 30 miles per hour, tore at the rock particles in which the plants subsisted. Many of the smaller grasses, particularly, were elevated on little pedicles of “soil,” the surrounding surface having been blown away. Most of these plants in the more exposed places would probably succumb to desiccation and wind scald even if they were not swept entirely out of the ground.

Considering these extreme conditions of “soil” and climate, it was a minor miracle that the higher plants had been able to gain a real foothold on the ash, pumice, and gravel. Some of my fellow members of the Katmai Project were amused by the botanist’s enthusiasm for the diversity of species and numbers of plants that we encountered in parts of the upper Valley. But when conditions were compared with Griggs’ description of the almost total lack of seed plants in 1930 “for miles around” the Novarupta area, it was realized that many plant colonists had successfully established themselves. The following list of species from the gravel-pumice area in the easternmost one-third of the Valley of Ten Thousand Smokes furnishes proof of the success of the invasion. The collections were made in 1953 and 1954, and undoubtedly included all the species that had gained a real foothold there since the 1912 eruption.

Pogonatum alpinum (alpine pogonatum)

Polytrichum commune (hair-cap moss)

P. juniperinum (juniper hair-cap moss)
Equisetum arvense (common horsetail), 5 localities
Agrostis scabra (tickle grass)
A. scabra var. *geminata* (tickle grass), 2 localities
Calamagrostis canadensis (bluejoint), 5 localities
Deschampsia caespitosa (tufted hair grass)
Trisetum spicatum (downy oat grass), 2 localities
Poa arctica subsp. *williamsii* (Arctic blue grass), 5 localities
P. hispidula (hispid blue grass), 2 localities
P. lanata (lanate blue grass)
P. stenantha (narrow-flowered blue grass)
Eriophorum angustifolium (tall cotton grass)
E. scheuchzeri (white cotton grass)
Carex macrochaeta (Alaska long-awned sedge), 2 localities
C. mertensii (Mertens sedge), 8 localities
Luzula arcuata (alpine wood rush), 3 localities
L. parviflora (small-flowered wood rush), 2 localities
Salix alaxensis (felty-leaved willow), 4 localities
S. anglorum (willow), 2 localities
S. arbusculoides var. *glabra* (willow)
S. arctica (Arctic willow), 2 localities
S. arctica var. *obcordata* (Arctic willow)
S. barclayi (Barclay's willow), 3 localities
S. desertorum (willow)
S. geyeriana (willow)
S. pseudomonticola (willow)
S. pulchra (beautiful willow)
S. scouleriana (willow)
Oxyria digyna (mountain sorrel), 4 localities
Sagina intermedia (snow pearlwort)
Papaver radiculatum subsp. *alaskanum* (Arctic poppy), 2 localities
Oxytropis (sp. ?) (oxytrope)
Epilobium latifolium (dwarf fireweed), 4 localities

Several small "islands" of plants at the very base of Mount Katmai should be mentioned before closing this section of my report. They were significant because they were almost certainly survivors of the pre-eruption vegetation. If this assumption is correct, these relicts afford information regarding the original plant cover of the area which was completely devastated before any botanist had seen and recorded it.

These plant "islands" were in the small canyon at the bottom of the valley between Knife Peak and Mount Katmai. (Pl. 7, fig. 2.) None of them exceeded a quarter of an acre in extent. Their survival appeared to be the result of two factors. First, much of the ash that fell directly onto them during the eruption could have been blown away by wind and carried off by the nearby stream. Second, jutting rock

promontories that stood above the colonies may have shielded the plants from later burial by landslides. These bluffs were so situated that they would have diverted the great masses of pumice which, for years after the eruption, continued to slide off the mountainsides into the valleys. The plants at the foot of these promontories were well supplied with moisture through seepage from the rock strata. At the time of my visit on August 7, 1954, the ground was covered with a luxuriant growth of plants. From one of the three or four of these original plant colonies in the southern portion of the canyon, the following 15 species were collected. Eight of them (marked with an asterisk) were not found anywhere else in the Valley of Ten Thousand Smokes.

- Schizogonium murale* (green algae)
- **Philonotis fontana* (moss)
- Equisetum arvense* (common horsetail)
- Agrostis scabra* var. *geminata* (tickle grass)
- Deschampsia caespitosa*, tufted hair grass
- **Stellaria crispa* (crisp starwort)
- **Cerastium caespitosum* (larger mouse-ear chickweed)
- Papaver radiculatum* subsp. *alaskanum* (Arctic poppy)
- **Cardamine bellidifolia* (alpine cress)
- **Saxifraga punctata* subsp. *nelsoniana* (brook saxifrage)
- Geranium erianthum*, northern geranium
- **Heuchera glabra* (alpine heuchera)
- **Epilobium hornemannii* (Hornemann willowherb)
- E. latifolium* (dwarf fireweed)
- **Romanzoffia sitchensis* (mist maid)

STUDY OF VEGETATION RECOVERY

In speculating about the invasion of the devastated area by low forms of plant life, Griggs expressed the wish that the whole sequence of organisms in the reestablishment of vegetation might be worked out. From such a study, he thought, one might gain a better understanding concerning the preparation of the earth for habitation by the higher animals and man.

Although some of the record had been lost in the 30 years between the National Geographic Society's major expeditions and the Katmai Project, it seemed desirable to begin in 1954 a systematic record of vegetation recovery in the area of "total" volcanism. Localities were selected in the valleys of the River Lethe and Knife Creek which were fairly representative in factors of plant growth. Six plots were established, three in each drainage. Most of the plots were located

in the upper portions of the watersheds, but two were placed at distances of 2 and 3 miles (air line) from the head of the valleys.

The plots were laid out as rectangles of approximately one-eighth acre in size. With one exception, the plots were 104.5 feet by 52.5 feet, or 5,486 square feet in area. The plot in the valley of the River Lethe near the northwestern spur of Baked Mountain (Plot C) was inadvertently laid out 109 feet in length instead of 104.5 feet. Its area was 5,723 square feet, or 278 square feet (5 percent) more than one-eighth acre.

The equipment available did not permit me to make highly accurate measurements, but they were probably sufficiently exact for the purpose. The 90-degree corners and directions of boundaries were laid out with a Brunton compass, using a declination setting of $22^{\circ}30'$ E. Sightings were made on conspicuous topographic features in order that the plots could be found more easily by future investigators. Because a staff or tripod was not available, the compass was placed on an empty ration carton in order to obtain the most accurate reading possible. The plot boundaries were measured with a 50-foot cloth tape.

Corners of the plots were marked by driving vertically lengths of $\frac{3}{4}$ -inch aluminum pipe which was furnished through the courtesy of the Fish and Wildlife Service. The pipe was driven at least 18 inches into the ground, while the portion above ground extended 3 to 4 feet. If rocks were available in the vicinity, they were piled around the base of the pipe for additional rigidity and to make the corners more conspicuous and easier to find in the future. It is possible that the winds which blow so fiercely at times in this area may disperse the rock piles, most of which were necessarily of pumice. It is believed, however, that the aluminum pipe will survive indefinitely even though it may be bent somewhat by the wind. In addition to being resistant to corrosion, the metal is likely to be kept fairly bright through abrasion by wind-blown pumice.

For ease in mapping and recording the vegetation and surface features, 2 cords marked at 5-foot intervals were used to subdivide the plot into 5-foot strips. After recording the plants within the first subdivision, the cords were moved progressively until the entire area had been covered. As a rule, the existing vegetation was so scant that individual plants could be recorded. The one exception, Plot B at the north base of the western spur of Broken Mountain, had a more luxuriant covering. It was possible with care, however, to obtain a close approximation of the number of plants even in the denser clumps. The location of plants of the various species, the washes or

temporary stream courses, and the outlines of exposed rock surfaces were mapped on coordinate paper. Charting was done by the writer, while an assistant aided by counting the number of individual plants and by checking species identifications and measurements. Record photographs were made with a Speed Graphic camera ($3\frac{1}{4} \times 4\frac{1}{4}$ inches); the negatives were numbered and deposited in the "wildlife division" photo collection of the National Park Service.

Aid in carrying equipment, laying out the plots, and mapping existing plant life was given by Messrs. George Schaller and Richard Ward. Robert Luntley also assisted in laying out Plot A. All this help is gratefully acknowledged.

DESCRIPTION OF PLOTS

PLOT A was established June 30, 1954. It was located on the broad ridge between the two principal forks or feeders of Knife Creek, and approximately one-half mile west of the foot of Fourth Glacier. It was on a south-facing slope of about 15 degrees, where the soil was a mixture of coarse sand and gravel. The long dimension of the plot (104.5 feet) was established on the magnetic north-south line. From the northwest corner of the plot, a line continued due north 59 feet intersected the northern edge of a steep bluff which formed the divide between the north and south forks of upper Knife Creek.

The following directional readings were made for me by Dr. Gar-niss H. Curtis, using a Brunton compass, from the northwestern corner of the plot:

Highest point on Whiskey Ridge (between Third and Fourth Glaciers),
S. 39° E.

North summit of Pt. 6281 on rim of Katmai Crater, S. 52°30' E.

Westernmost summit of Trident group, S. 11°0' W.

Northwestern summit of Knife Peak, N. 2°30' E.

Junction of north and south forks of Knife Creek (approximate direction),
S. 73° W.

North rim of Katmai Crater, S. 82° E.

Northeast corner of plot (backsight), S. 66°30' E.

Circumstances made it necessary to defer the mapping of the vegetation until August 4, 1954. Tickle grass (*Agrostis scabra* var. *geminata*) was the dominant species with 367 plants. The only other species found, the alpine wood rush (*Luzula arcuata*), was represented by four individuals. (Fig. 1.)

Record photographs were made August 4, 1954, from the southeast corner of the plot to the southwest corner (negative No. 12,090) and to the northwest corner (No. 12,082). Another set of photographs was made from the northwest corner of the plot to the northeast



☞ Tickle Grass, symbol represents ten plants, unless designated by numbers

• Alpine Wood Rush

FIG. 1.—Diagram of Plot A and distribution of plants. Head of Knife Creek, August 4, 1954.

corner (No. 12,086) and to the southeast corner (No. 12,083). Additional pictures were taken August 7 from near the southeast corner toward the southwest corner (Nos. 12,010 and 12,093), and from near the northwest corner toward the northeast corner (No. 12,078).

Plate 9, figure 1, shows the northern portion of the plot and the desolate character of the area as it appeared on August 7, 1954 (No. 12,078).

PLOT B was established August 6, 1954, in the valley of upper Knife Creek. It was at the north base of Broken Mountain, 1 to 2 miles east of the western tip of the main ridge of Broken Mountain. The plot was on a wide outwash plain which sloped gently northward from the base of the mountain to Knife Creek, and was between one-quarter and one-half mile from the stream. The terrain was fairly uniform, with numerous broad, very shallow washes which were no more than a few inches deep. The soil was comparatively uniform in composition, being fine to coarse punice, with some gravel but no rock larger than an estimated 3 to 4 inches.

The plot was laid out with its long axis in an east-west direction and at approximately right angles (90 degrees) to the slope. Directional readings were made with a Brunton compass from the southeastern corner of the plot:

Easternmost high point at summit of Knife Peak, N. 28° E.

Westernmost sharp peak (unnamed) on long ridge north of Knife Creek and the River Lethe, and west of Knife Peak, N. 43° W.

Westernmost high point on ridge of Buttriss Range, N. 90° W.

Outlet of small lake (unnamed) which was immediately north of and emptied into Knife Creek, N. 1° E.

Plot B contained much more plant life than any other area that was selected for permanent designation and study. In addition to mosses, which were limited to two small areas and were not identified, five species were present. Four of these were grasses or grasslike herbs. The most abundant were the alpine wood rush (*Luzula arcuata*) with approximately 473 individual plants, and bluejoint (*Calamagrostis canadensis*) with about 309 plants on the plot. Arctic blue grass (*Poa arctica* subsp. *williamsii*) was represented by 86 individuals and Mertens sedge (*Carex mertensii*) by 31. It was impossible to determine accurately the number of individual specimens in the larger clusters or mats of *Calamagrostis* without tearing up and destroying the plants, so distinct stems were totaled in five places. These clumps are distinguished on the plot diagram by underlined numbers. Eighty-three plants of mountain sorrel (*Oxyria digyna*) were found, mainly in a narrow band down the center of the plot. (Fig. 2.)

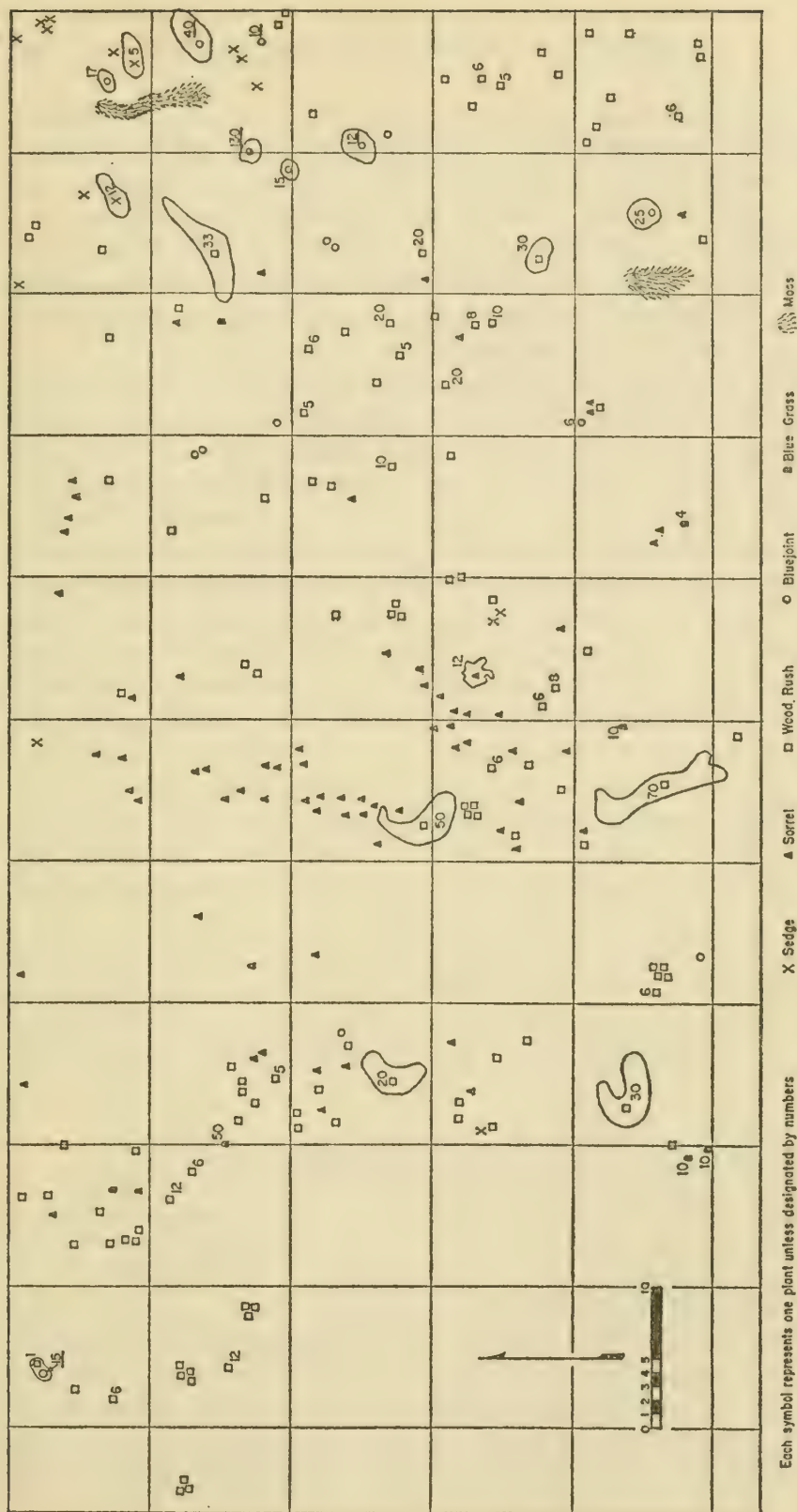


FIG. 2.—Diagram of Plot B and distribution of plants (scale at lower left in feet). North base of Baked Mountain, August 6, 1954.

Photographs were taken on the same date (August 6) as follows: From the southwest corner of the plot east to include both eastern corners (No. 12,059); from a point about 75 feet west-southwest of the southwest corner to include the entire plot (No. 12,075); in a northeastern direction from a point about 75 feet south of the southwest corner of the plot (No. 12,076); and southeast from a point about 75 feet north of the northwest corner of the plot (No. 12,072). (The last-mentioned is reproduced as pl. 9, fig. 2.)

PLOT C was laid out August 6, 1954. It was in the broad, nearly flat valley east of the River Lethe and near the base of the most northwesterly spur of Baked Mountain. The site selected was between one-quarter and one-half mile west of the 2,000-foot contour at the foot of the mountain. At this point the slope of the valley floor was almost imperceptible, and erosion of the surface was reduced to sheet washing and a few tiny rills an inch or two in depth. The site was composed of volcanic tuff which was hard and pavementlike. Over wide areas the tuff was covered by a layer of granular pumice about an inch deep which had been washed down from the slope of Baked Mountain. The pumice ranged in size from very coarse sand to pebbles an inch or two in diameter.

The plot was 52.5 by 109 feet, with the long dimension directed to the magnetic north. This was at an approximate right angle to the very gradual slope westerly down to the River Lethe. Because of the absence of large pumice fragments in the area, the aluminum corner posts could not be augmented by piles of rock.

Owing to the low cloud ceiling that prevailed at the time the plot was established, compass readings were restricted to topographic features at the bases of the surrounding mountains. The features and their magnetic bearings from the southwestern corner of the plot were as follows:

- Northwestern point of the base of Buttress Range, N. 65° W.
- Largest canyon in eastern slope of Buttress Range, S. 30° W.
- North base of Mount Cerberus, S. 42° E.
- Active fumarole area at southwestern base of Baked Mountain, S. 42° E.
- Foot of largest glacier which descended the north slope of Mount Mageik (perhaps from the basin between Mount Mageik and Mount Martin), at the southwestern head of Lethe Valley, S. 5° W.

No plant life of any kind was found on the plot or in the vicinity.

Photographs were made from two points: From the northwest corner of the plot in a southerly direction to include the southeast and southwest corners (Nos. 12,085 and 12,091); and from the southwest corner in a northerly direction to include the northeast and

northwest corners of the plot (Nos. 12,047 and 12,055). Because of weather conditions, topographic features more than a mile distant did not register on the film. However, the area in and close to the plot was recorded satisfactorily.

PLOT D was established August 8, 1954, on the floor of the River Lethe valley about 2 miles south of the preceding plot. Plot D was on a gentle west or southwest slope about one-half mile below (southwest of) the active fumarole area on the southwestern base of Baked Mountain. The long axis was north-south, at approximately right angles to the slope. The site was north of the wide wash that drained the valley between Baked Mountain, Novarupta, Falling Mountain, and Mount Cerberus.

The terrain and ground character were similar to those on the preceding plot except that the coating of rotten pumice over the consolidated tuff was deeper on Plot D. Less washing was evident, owing perhaps to the wide watercourse a short distance to the south which captured much of the up-slope run-off. The granular pumice was mostly coarse—one-quarter to 1 inch in diameter. Rocks larger than 3 inches were rare. "Drifts" of pumice in broad depressions in the tuff were 2 to 4 inches deep, while the layer on more wind-swept places was very thin.

A low cloud cover limited the sight readings which could be taken to orientation points in the near vicinity. Those made from the southeastern corner of the plot were as follows:

Lowest point in saddle between Falling Mountain and Mount Cerberus, S. 60° E.

V-notch in moraine in front of base of glacier at west side of Mount Mageik, S. 30° W.

Junction, on skyline, of the northeastern slope of Mount Katolinat and the west ridge of the unnamed mountain west of Knife Peak and south of Mount Ikagluik, N. 41° W. (Note: This point was a *projection* of the silhouette of the ridge about 3 miles east of the junction of Knife Creek and Ukak River, against the more distant outline of Mount Katolinat.)

Top of rock cliff above the long cinder slope at the most western end of Buttress Range which was visible from the southeastern head of Lethe Valley, N. 53° W.

Two duplicate sets of photographs were made which showed the plot clearly, but only the lower slopes of mountains in the background registered. From a point 30 feet south of the southeast corner of the plot, Nos. 12,030 and 12,031 were directed to the north-northwest toward the northwestern base of Baked Mountain, and included all except the extreme southwest corner of the plot. The second set of pictures, Nos. 12,006 and 12,008, showed the view south-southwest

to the base of Mount Mageik and included all the plot except the extreme northwestern corner.

PLOT E (fig. 3) was established August 8, 1954, on the slope below the western base of the lava plug in Novarupta. The site was approximately one-fourth mile from the lip of the cup into which the plug extruded. The area was a gentle westerly slope of relatively fine black ash or pumice which was furrowed by many erosion gullies. Numerous chunks of porous rock, probably "bombs" thrown from Novarupta in the terminal phase of the eruption, littered the terrain. The rocks ranged in size up to 2 and occasionally 3 feet in diameter. (The plot was located apparently in the densest portion of the steam in Griggs' 1919 photograph entitled "Falling Mountain from across the Valley." Griggs, 1922, "The Valley of Ten Thousand Smokes," p. 220.)

The plot was laid out with its long axis on the magnetic north-south line. Corners were marked by aluminum pipes, around which rocks were piled. The drainage within the plot was approximately southwest. The slope of the general area, however, was more to the west or even northwest down to the broad valley between Broken Mountain, Baked Mountain, and Falling Mountain. Within the plot were two watercourses which were dry, of course, except during heavy rainstorms. The shallower drain was only 2 to 4 inches deep; it was irregular and probably shifted about with each flood. The second, more permanent gully was 8 inches deep at the upper side of the plot, but deepened to $2\frac{1}{2}$ feet at the lower boundary. Evidences of washing indicated that during severe downpours, water flowed in sheets over much of the area.

Sight readings were made under difficulties, owing to low cloud cover, from the southeastern corner of the plot to the following landmarks:

South base of Novarupta's volcanic plug, as visible above the earthen rim of the crater, S. 83° E.

Cone-shaped "plug" near east base of avalanche area at foot of Falling Mountain, S. 49° E.

West base of avalanche scar on Falling Mountain, S. 3° E.

Base of glacier on west slope of Mount Mageik, S. 36° W.

Base of rocky area on southwest spur of Baked Mountain (above fumaroles, which were hidden by the spur), S. 70° W.

Plant life on the plot was sparse and confined largely to the areas, such as along washes, where moisture was retained longest. In addition to a patch of moss of unidentified species about 1 by $1\frac{1}{2}$ feet in extent, the only vegetation on the plot was a sedge, *Carex mertensii*.

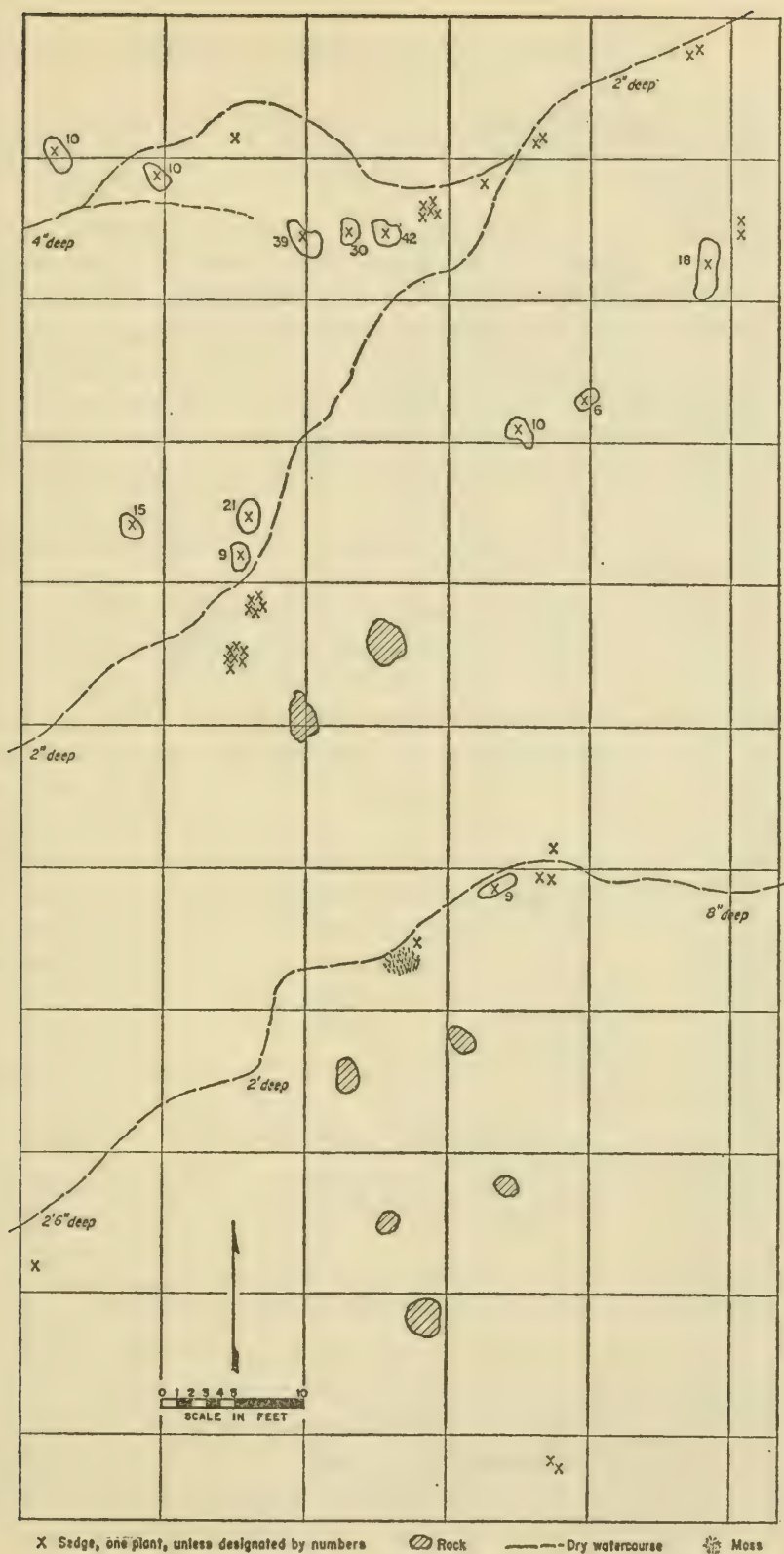


FIG. 3.—Diagram of Plot E and distribution of plants. Novarupta, August 8, 1954.

This species occurred chiefly in clumps or groups of individuals which were difficult to count accurately. According to our tally, the total was 250 plants.

Photographs were made from three points: (1) looking north-northeast from about 30 feet south of the southwest corner of the plot, across the plot toward the west base of Novarupta (photographs Nos. 12,012, 12,014, and 12,018); (2) looking south-southeast from a point about 75 feet north of the northwest corner of the plot, with the avalanche-scarred base of Falling Mountain in the background (photographs Nos. 12,016 and 12,020); and east across the central portion of the plot to the lava plug of Novarupta in the background (photograph No. 12,017). (See pl. 10, fig. 1, No. 12,016.)

PLOT F was laid out August 9, 1954, on the first gravel-pumice flat above and north of Knife Creek, about one-half mile north of the junction of the north and south forks of the Creek. The site was east of a low ridge which extended in a northerly direction from the creek junction to the foot of Knife Peak. The terrain was quite uniformly flat with no evident slope, and no washes more than an inch or two in depth were on or near the plot. The ground was thickly sprinkled with rounded pieces of pumice up to 3 inches in diameter.

The plot was laid out with its long axis on the east-west magnetic line. Sizeable rocks being completely lacking, the corners were marked solely by pipes. Compass readings to prominent topographic features in the vicinity were made from the northwest corner under favorable atmospheric conditions and were as follows:

South summit of Knife Peak, S. 13° E.

Summit of north ridge of unnamed mountain between Number Three Glacier and Number Four Glacier, S. 68° E.

Summit of knoll forming west end of ridge between the north and south forks of Knife Creek, S. 80° E.

Summit of sharp rocky knoll at south end of low ridge that extended from foot of Knife Peak to junction of north and south forks of Knife Creek, S. 18° W.

Point of ridge that extended west from westernmost mountain between Number Four Glacier and Number Five Glacier, N. 76° E.

No vegetation of any kind was growing on the plot. (Pl. 10, fig. 2.)

Photographs were made from two points: (1) looking west-southwest from a point 25 feet east of the northeast corner, across the plot toward the junction of the north and south forks of Knife Creek and of the western base of Broken Mountain (photograph No. 12,045); and (2) looking east-northeast from a point about 25 feet west of the

southwest corner, across the plot toward Mount Katmai and Knife Creek Glaciers Numbers Four and Five (photograph No. 12,063). The latter is reproduced in this report as plate 10, figure 2.

III. THE BIRDS

REMARKS AND ACKNOWLEDGMENTS

Many observations of birds were recorded during the two seasons of the Katmai Project as well as during the period that I was in the Monument during 1940. I kept systematic notes on localities, ecological habitats, and abundance or, in some cases, actual numbers of individuals. Several of my associates, who are mentioned below, contributed additional notes.

The information has been narrated as concisely as possible in the species accounts that follow. These accounts include, in addition to the records obtained during 1953 and 1954, brief summaries of my observations of September-October, 1940. I have also included notes from the work of W. H. Osgood in 1902 and of James S. Hine in 1917, as well as records and observations by Ira N. Gabrielson who visited the Brooks Lake area briefly in 1940 and 1946. (Gabrielson and Lincoln, 1959.) Robert Ridgway, while a member of the Harri-man Alaska Expedition, collected a number of birds at Kukak Bay in July 1899. A few specimens also were taken at Katmai by Clarence F. Maynard, topographer of the National Geographic Society's expedition in 1917. Thus the accounts comprise a digest of the past records as well as new information on the birds of Katmai National Monument.

The periods of observation (late June to early October) have been ample for making a record of the bird life of the Monument during summer and much of the fall. Records are completely lacking, however, for the winter and spring seasons. The latter is particularly important in affording opportunity to observe the northward migration and arrival of summer residents, as well as the beginning of nesting activities. All summer resident species had arrived in the Monument each year prior to the commencement of our fieldwork. Doubtless this wide gap in our knowledge of birds in the area will be filled eventually.

Appreciation is expressed for permission to use a considerable number of data which were accumulated during the 1954 field season by Dr. Gerald L. Brody, of Ann Arbor, Mich., and by my assistant, George B. Schaller. Several notes also were contributed by Richard Ward, supervisory ranger in charge of the Monument in 1954. Notes

on bird observations in the previous season were given to me by Garniss Curtis, Everett L. Schiller, Robert Johnsrud, and Ronald Kistler, all of the Katmai Project, and by George Peters, Assistant Chief Ranger of Mount McKinley National Park and supervisory officer at Katmai National Monument during the summer of 1953. I am grateful also to Ira N. Gabrielson for permission to utilize his field notes of 1940 and 1946. In all these cases the observations have been credited to the respective observers.

Finally, I am greatly indebted to Frederick C. Lincoln, of the U. S. Fish and Wildlife Service, for advice on nomenclature and permission to consult the records (then unpublished) of the American Ornithologists' Union Committee for the fifth edition of the "Check-List of North American Birds." This assistance, and information from the manuscript on Alaskan birds by Gabrielson and Lincoln (since published as "Birds of Alaska," 1959) which was generously provided by the latter, did much to increase the value of the following accounts.

The catalog of Katmai birds includes 117 species on the basis of specimens or sight records. Eight additional forms are placed in a hypothetical list because they have been recorded in environments similar to those in the Monument and within 20 miles of the boundaries. The Katmai Project was responsible for adding 37 species of birds to the number previously known from this area. Of these additions, 33 were identified during the first season and the remaining 4 in the second year of operation.

ENVIRONMENTAL DISTRIBUTION

Notes on the environment in which various species were found have made it possible to list the birds according to their habitat preferences. This has been done for all species on which sufficient data were obtained; those birds which were recorded only a few times have been omitted. Birds which were observed frequently in more than one habitat will be found under the several headings.

BIRDS OF THE INLAND LAKES AND STREAMS

This environment included ponds of small size as well as the larger lakes which covered many square miles. The streams ranged in size from creeks a few feet across to rivers of considerable volume. Practically all the waters were cold and most were clear. However, some lakes such as Iliuk Arm were cloudy with glacial silt, and certain streams (including Savanoski and Ukak Rivers) carried heavy loads of pumice. Most, but not all, of the birds named below spent their



1. Takli Island, in Amalik Bay, was covered by 2 to 3 feet of ash during the Katmai eruption of 1912. By early October, 1940, when this picture was made, grasses and green alder had occupied an estimated 50 percent of the area. The tallest alders were 3 to 4 feet high.



2. A nearby area on Takli Island was photographed July 28, 1953. Over 90 percent of the island had been covered by vegetation, and numerous additional species had invaded since 1940. Alders grew 8 feet tall. Flat area in left foreground was bare sand in 1940; by 1953 it was covered by a dense sod of *Calamagrostis*.



1. Plot A for study of revegetation, near head of Knife Creek, photographed August 7, 1954. Base of Knife Peak at left and of Mount Katmai at right. Tickle grass and alpine wood rush were present but are not discernible in the picture. (See pp. 74-76.)



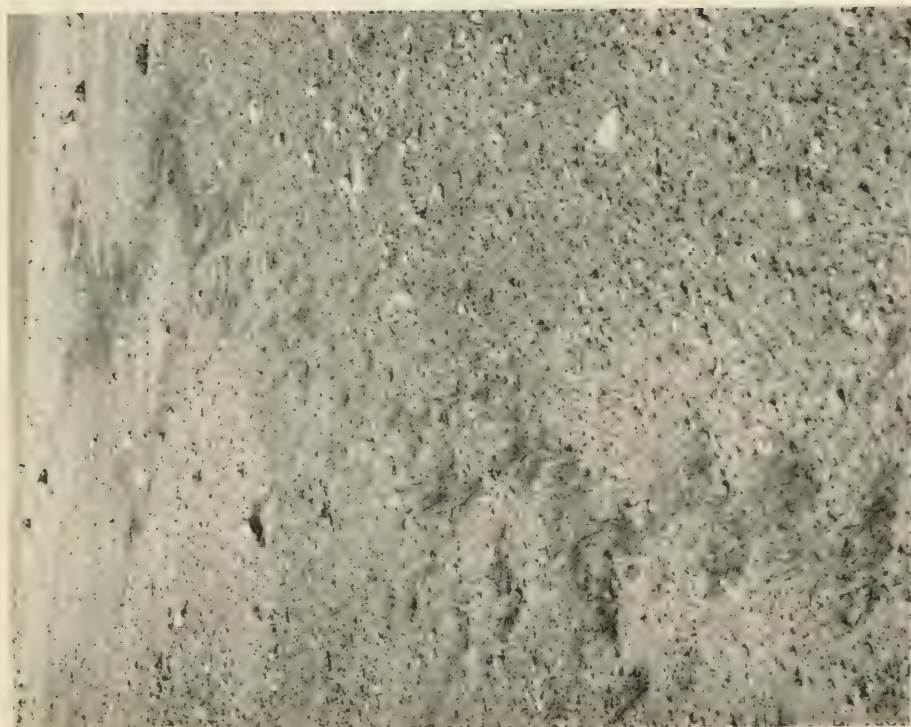
2. Plot B for study of revegetation, in valley of upper Knife Creek at the north base of Baked Mountain. Photographed August 6, 1954. Two small patches of moss and five species of higher plants were present. The most abundant were alpine wood rush and bluejoint. (See pp. 76-78.)



1. Plot E for study of revegetation, about one-quarter mile west of lava plug in Novarupta. Photographed August 8, 1954. Base of Falling Mountain in background. One species, Mertens sedge, had gained a foothold. (See pp. 80-82.)



2. Plot F for study of revegetation, in upper valley of Knife Creek, was completely barren of plant life. Photographed August 9, 1954, looking east-northeast toward Mount Katmai and Glaciers III and IV (in background). Between the glaciers is Whiskey Ridge. (See pp. 82-83.)



1. Plant survival was difficult on the area devastated by volcanic action because water drained rapidly through the pumice. Shallow depressions, which held moisture longest, were nurseries for pioneer plants. (See p. 70.) Head of Knife Creek, August 1, 1954.



2. Young double-crested cormorants at nest on an island in Hink Arm. September 1, 1954.

lives on this aquatic habitat. In some cases, the birds were equally at home on marine waters.

Pacific loon	Red-breasted merganser
Red-throated loon	Northern bald eagle
Holboell's grebe	Osprey
Double-crested cormorant	Glaucous-winged gull
Whistling swan	Herring gull
Common mallard	Bonaparte's gull
Pintail	Arctic tern
Green-winged teal	Western belted kingfisher
Baldpate	Northern dipper
Greater scaup	Grinnell's northern water thrush
Barrow's golden-eye	Rusty blackbird
White-winged scoter	

BIRDS OF FRESH-WATER BEACHES AND MUD FLATS

Sand or gravel beaches fringed the larger lakes and, with mud flats, occurred sporadically along some of the stream banks. Most of the bird species listed below were characteristic of and practically limited to this environment and/or to marine shorelines. In addition, most of the species named under "Birds of the Inland Lakes and Streams" were seen very frequently resting or feeding on the lake shores.

Semipalmated plover	Lesser yellow-legs
Pacific golden plover	Least sandpiper
Black turnstone	Northern common raven
Spotted sandpiper	Western water pipit
Greater yellow-legs	

BIRDS OF MARINE COASTAL WATERS AND BAYS

This habitat was confined to the coast of Shelikof Strait and Cook Inlet. The shores were mostly rocky with frequent steep bluffs and headlands and deep, fiordlike bays. Broad, sandy beaches and gradually shelving shorelines were also present, however, such as those at Kaguyak, Hallo, and Katmai Bays. The species named below were characteristic of, although not always limited to, this aquatic environment.

Pacific Arctic loon	Greater scaup
Red-throated loon	Barrow's golden-eye
Holboell's grebe	Steller's eider
Horned grebe	King eider
Double-crested cormorant	White-winged scoter
Pelagic cormorant	Surf scoter
Common mallard	Common scoter

Red-breasted merganser	North Pacific murre
Northern bald eagle	Pigeon guillemot
Osprey	Marbled murrelet
Northern phalarope	Horned puffin
Glaucous-winged gull	Tufted puffin
Herring gull	Western belted kingfisher
Bonaparte's gull	

BIRDS OF MARINE BEACHES AND MUD FLATS

Stony or sandy beaches and mud flats were not extensive on much of the open coast of Shelikof Strait, where the steep mountains and headlands generally plunged into deep water. However, fine beaches were found in several of the bays, and mud flats occurred at the mouths of some rivers and elsewhere depending on tide conditions. Some of the birds listed under "Birds of Marine Coastal Waters and Bays," especially the various gulls, often rested or searched for food on the beaches.

Black oystercatcher	Greater yellow-legs
Semipalmated plover	Aleutian red sandpiper
Black turnstone	Western sandpiper

BIRDS OF THE SPRUCE FOREST

This environment was extensive on the western slope of the Monument where white spruce abounded (pl. 3, fig. 1) but was limited to a few relatively small areas of Sitka spruce along Shelikof Strait. It was a lowland type and rarely extended unbroken above 600 or 700 feet elevation. While the list of birds found in this habitat is comparatively brief, some of the species were so partial to spruce forest that they were rarely or never found elsewhere. Among these were the spruce grouse, three-toed woodpecker and white-winged crossbill. The birds recorded are:

Alaska spruce grouse	Alaska myrtle warbler
Alaska three-toed woodpecker	Northern pileolated warbler
Alaska gray jay	Common redpoll
Yukon chickadee	American white-winged crossbill
Boreal chickadee	Slate-colored junco
Eastern robin	Western tree sparrow
Western golden-crowned kinglet	Gambel's white-crowned sparrow

BIRDS OF COTTONWOOD GROVES

Few areas of this type in the Monument exceeded 100 acres in extent. Cottonwood groves were found from sea level to approxi-

mately 500 feet elevation. The type was relatively open, often with a thin understory of young cottonwoods, willow clumps, and alder, and the ground was generally covered with dense, tall grass and other herbs. (Pl. 5, fig. 1.) Its bird fauna was usually sparse. Those recorded in that type are:

Horned owl	Northern pileolated warbler
Alaska gray jay	Western tree sparrow
Yukon chickadee	Gambel's white-crowned sparrow
Boreal chickadee	Golden-crowned sparrow
Northern varied thrush	

BIRDS OF ALDER THICKETS

Dense thickets of alder were usually limited in area but were widely distributed on both sides of the Aleutian Range from sea level to altitudes of nearly 2,000 feet. Alder was rarely mixed with other shrubs. The bird life was limited in population and in species to sparrows, thrushes, and chickadees.

Yukon chickadee	Western tree sparrow
Boreal chickadee	Gambel's white-crowned sparrow
Northern varied thrush	Golden-crowned sparrow
Alaska hermit thrush	Aleutian song sparrow
Slate-colored junco	

BIRDS OF WILLOW THICKETS

This type of environment was widely distributed in the lowlands, usually below 1,000 feet altitude. It was not extensive in area and often was interspersed with other vegetation types, especially grassland. Birds seen in willow thickets were:

Grinnell's northern water thrush	Western tree sparrow
Northern pileolated warbler	Gambel's white-crowned sparrow
Savannah sparrow	Aleutian song sparrow
Slate-colored junco	

BIRDS OF MIXED DECIDUOUS WOODS-GRASSLAND

The vegetation of this habitat was chiefly willow, alder, and *Calamagrostis* grass, but many other species also occurred. As its name implies, the type was a mixture of plant composition and formations. It included all gradations between closed woodland and open grassy meadows, and ranged in elevation from sea level to 1,500 feet or more. A scene in extensive grassland on low-altitude tundra is shown in plate 4, figure 1. None of the bird species recorded was limited solely

to this type. The sparrows and willow ptarmigan were the most characteristic.

Willow ptarmigan	Savannah sparrow
Alaska gray jay	Slate-colored junco
Yukon chickadee	Western tree sparrow
Boreal chickadee	Gambel's white-crowned sparrow
Northwestern great shrike	

BIRDS OF MARSHES AND BOGS

Although rather numerous, most of the marshes and bogs in the Monument were small and their distinctive bird fauna was limited to the four species named below. The most extensive grassy marshes were found on the western shore of Lake Coville and in Swikshak Lagoon. Bogs, usually of the spruce type, were frequent over the lowlands in the western part of the Monument. (Pl. 3, fig. 2.)

Marsh hawk	Greater yellow-legs
Wilson's common snipe	Lesser yellow-legs

BIRDS OF THE HIGH TUNDRA

The open grassland (pl. 4, fig. 2) began at elevations above 1,200 feet and continued upward to permanent snowfields. The grasses and other herbs were short and sometimes sparse, while alder and willow shrubs were limited to depressions where they could find shelter from the winds. The habitat was bleak, cold, and often windy. While the bird species were few, several of them (i.e., longspurs, pipits, and finches) were represented by large numbers of individuals. Birds recorded on the tundra are:

Goshawk	Hepburn's gray-crowned rosy finch
Marsh hawk	Savannah sparrow
Nelson's rock ptarmigan	Golden-crowned sparrow
Northern common raven	Alaska Lapland longspur
Eastern robin	Eastern snow bunting
Western water pipit	

BIRDS RECORDED IN VALLEY OF TEN THOUSAND SMOKES

This list includes species seen on or over areas on any of the headwaters of the Ukak River that were deeply covered by the "sand flow" and pumice deposits of the 1912 eruption. While the "type" of habitat was local, special interest is attached to it because all the original bird life was eliminated by the eruption. The resulting inhospitable environment prevented most species from returning, and the appearance

of any bird there was a matter of special note. Therefore, the specific locality and date of the observation follow each species.

Green-winged teal. Head of the River Lethe valley, mid-August, 1954 (Curtis).

American rough-legged hawk. Near Three Forks (lower valley), September 14-17, 1940 (Cahalane, 1944, p. 362).

Golden eagle. West slope of Katmai Volcano, July 4, 1954 (Curtis).

Northern bald eagle. "Over valley," summer, 1917 (Hine, 1919, p. 475).

Marsh hawk. Lower end of valley, September 15, 1940 (Cahalane, 1944, p. 363).

Willow ptarmigan. Upper Knife Creek, early August, 1954 (Curtis and Schaller).

Northern common raven. Upper Knife Creek, about August 15, 1954 (Curtis).

Western water pipit. Upper Knife Creek, August 5, 1954 (Schaller).

Common redpoll. "Over valley," summer, 1917 (Hine, 1919, p. 483).

Golden-crowned sparrow. Head of Knife Creek, early August, 1953 (Johnsrud).

Eastern snow bunting. "Valley," and head of Knife Creek, summer of 1917, and numerous occasions in July and August, 1953 and 1954 (Hine, 1919, p. 476, and Cahalane).

BIRDS THAT OCCUR CHIEFLY AS FALL MIGRANTS

This list is appended for the information of persons who may be in the Katmai area in late summer or fall (after August 20) and wish to know the species that are most numerous at that season. Many of these birds may be found here in early or midsummer, but at best they are relatively scarce until the southward migration begins.

Holboell's grebe	Ruddy duck
Horned grebe	Goshawk
Canada goose (or related race)	Black turnstone
Pintail	Bonaparte's gull
Greater scaup	North Pacific murre
Barrow's golden-eye	Marbled murrelet
Harlequin duck	Horned puffin
Steller's eider	Northwestern great shrike
King eider	Alaska yellow warbler
Surf scoter	Alaska myrtle warbler

ANNOTATED LIST

Gavia arctica pacifica (Lawrence), Pacific Arctic loon. This, the most common species of loon, was not numerous. I recorded its presence only five times in 1953 and on seven occasions in 1954. The largest number of birds seen in one area was six. Dr. Brody recorded that

number on Naknek Lake, August 17, 1954, and I saw six loons on Brooks Lake, August 31 (1954).

The Pacific loon apparently moves in autumn from the interior out to the coast, for in September-October, 1940, I recorded it as "common" and "abundant" from Kinak Bay to Katmai Bay. It was not seen on the coastal waters during July-August (1953) nor on the inland lakes after September 9 (1940).

During the summers of 1953-1954 Pacific loons were noted on Brooks, Grosvenor, and Coville Lakes, Iliuk Arm, and the North Arm of Naknek Lake. The altitude of all these bodies of water is under 200 feet. The earliest observation of this bird was on June 29 (1953), the latest on October 7 (1940).

Gavia stellata (Pontoppidan), red-throated loon. The species was scarce during the summer months, particularly on the inland lakes. It was seen there only five times throughout the two field seasons. All these observations were made between August 18 and September 1 on Naknek Lake and the North Arm.

The red-throated loon was a little more numerous in summer along the coast of Shelikof Strait. There I saw one bird on a pond and several flying over lower Katmai River, "a very few" in Kukak Bay, and "several" at Cape Douglas. On October 4, 1940, the species was rather numerous from Amalik Bay to Katmai Bay.

Podiceps grisegena holböllii Reinhardt, Holboell's red-necked grebe. Apparently rare during the summer, this species moves into the Katmai area in autumn. Schaller saw a red-necked grebe diving for fish in Grosvenor Lake on July 24, 1954. Brody observed one bird, in full plumage, August 24 and 30, 1954, on a small lake about a quarter of a mile east of the mouth of Brooks River. I found the birds common on the northeastern portion of Lake Coville, September 2, 1953. They were abundant along the coast of Shelikof Strait between Katmai and Kinak Bays when I cruised these waters early in October 1940. A leg bone of a red-necked grebe was picked up in the interior of Kuikpalik Island, July 29, 1953, by our helicopter pilot, Don Williams. Since the island was well stocked with foxes, the bird may have been killed or picked up as carrion by one of these carnivores.

Podiceps auritus cornutus Gmelin, American horned grebe. The species appears to be a fall migrant in this area, where it is virtually limited to coastal waters. The only inland record comes from Brooks

Lake, where I saw one bird September 9, 1940. Early the following month great numbers were seen on Shelikof Strait and in most of the inlets from Katmai Bay to Kinak Bay.

No horned grebes were observed during the period of the Katmai Project, with the possible exception of two birds which were glimpsed by Schaller for a few moments August 21 on Naknek Lake. They were in view too briefly for him to be positive of the identification.

Phalacrocorax auritus cincinatus (Brandt), northwestern double-crested cormorant. It is presumed that all cormorants seen by us belonged to this species. The birds were noted often throughout the summer, although it was seldom that more than a half-dozen were seen in a day on any of the inland lakes. During this period the species was somewhat more numerous on Shelikof Strait and in the coastal bays, probably because of better opportunities for nesting and feeding.

As they began to move about more, cormorants were seen in larger numbers in the fall. I found them numerous on Lake Coville and the North Arm of Naknek Lake early in September, 1953. From observations in 1940 it was concluded that cormorants increased on inland waters up to about September 25 and then became relatively scarce. In the bays off Shelikof Strait, however, the species was termed "common to abundant" between October 4 and 7.

One and three nests, respectively, were found on the two largest islands in the western portion of Iliuk Arm. A small colony was located on an eroded rock pillar (portion of a dyke) on the north shore of Kukak Bay. (Pl. 11, fig. 2.) When I examined it from a boat at a distance of about 100 feet on August 6, 1953, some 12 nests containing young of various sizes were visible. Other nests had already been vacated. Judging from this evidence and the number of adults and flying juveniles, it would appear that the colony had been made up of at least 25 nesting pairs.

The nesting of the double-crested cormorant extends over much of the warmer months. Vacated nests and free-swimming juveniles were seen in Iliuk Arm on July 16 (1954), while two eggs in a nest on an island about 2 miles east of the Narrows did not hatch until about August 12 and August 17, respectively. By September 1 the two young were covered with down but the younger bird had not developed sufficiently to show fear when we approached. (Pl. 11, fig. 2.)

Cormorants in Iliuk Arm were associated with glaucous-winged gulls and nested on small islands in close proximity to that species.

Phalacrocorax pelagicus pelagicus Pallas, pelagic cormorant. I did not identify the species during any of my three stays in Katmai Monument, but Hine (1919, p. 479) found that "colonies of this cormorant nested on the shelves of the sea wall along Katmai and Kashvik Bays" during the 1917 season. Gabrielson (Gabrielson and Lincoln, 1959, p. 97) "recorded it as common . . . at various places along the Alaska Peninsula."

Olor columbianus (Ord), whistling swan. The optimum habitat of this graceful bird was east and southeast of the Bay of Islands. Between the Bay and Savanoski River was an extensive area of marshes sprinkled with many ponds and small lakes. Throughout much of the nesting season, more than 50 square miles was either under water or so wet as to be unattractive hunting grounds for most mammalian predators. Protection as well as aquatic food thus was provided for swan families. The area was approximately 50 feet in altitude.

Despite the suitability of this area east of the Bay of Islands, swans were not numerous during the nesting season. Our maximum count of birds in one day (which included a helicopter flight over a portion of the marshes) was 11 adults and 3 young on August 16, 1953. The largest family of cygnets seen numbered 6 (September 2, 1953, in the Bay of Islands). Schaller disturbed 5 juveniles with their parents into flight from a pond near lower Contact Creek on September 5, 1954.

The lower reaches of the Savanoski River were favorite resting places of whistling swans after mid-August and throughout September. We often saw the birds sleeping or preening their feathers on the mud bars opposite our camp about a mile above the river's mouth.

Late in the summer, much larger numbers of swans frequented the Naknek River below the rapids about 20 miles west of the Monument. Schaller estimated 150 birds in a quiet eddy near King Salmon on September 6, 1954.

Branta canadensis (Linnaeus), Canada goose (or related race). In one of its several forms, the Canada goose occurred in the Katmai area on rather rare occasions early in the fall. I saw a group of about 40 birds flying up Savanoski River on August 29, 1953, and the following day a flock which approximated 100 individuals was seen pursuing the same course. The valley was a natural flight course between Bristol Bay and Cook Inlet.

Anas platyrhynchos platyrhynchos Linnaeus, common mallard. Although far from being the most numerous duck, the mallard was widespread in the Monument and was seen oftener than any of the waterfowl except the red-breasted merganser. My field record shows that mallards were seen on 13 occasions during the 1953 season, although they were listed only 4 times the following year. The species occurred in small numbers—2's and 3's or families, but never exceeding 8—up to the end of August.

Migrants swelled the population appreciably after September 1. I found mallards numerous September 2, 1953, in the marshes at the head of Lake Coville and on American Creek for several miles upstream from the lake. The species was also abundant along the coast of Shelikof Strait in September and early October, 1940, when hundreds were seen at the head of Geographic Harbor and lesser numbers in Amalik and Kinak Bays.

Mallards were found on all types of water—sloughs, marshes, streams, large and small lakes, and the bays off Shelikof Strait. None was seen at elevations exceeding 500 feet. The most favorable areas for nesting or feeding that I found were the marshes at the west end of Lake Coville and the sloughs in the lower valley of Katmai River. The flats between the Bay of Islands and Savanoski River, northeast of Mount LaGorce, appeared to be excellent habitat. Owing to the difficulty of travel in this marshy region, more specific information could not be gathered.

The groups of young mallards that were identified as broods numbered as follows: 7 on a pond a quarter of a mile east of the mouth of Brooks River July 15; 4 on a pond at Kaguyak July 29; and 8 (probably) on Brooks River September 1. Mallards were seen by Brody in association with pintails and green-winged teals in sloughs and marshes around the mouth of Brooks River.

Anas acuta Linnaeus, pintail. From the evidence available, the pintail was a fall migrant within the Monument. The earliest seasonal record was made by Schaller August 17, 1954, with a lone bird on Naknek Lake. A family consisting of female and seven young appeared two days later in the sloughs near the mouth of Brooks River, and we saw them there frequently over the next two weeks. We observed a group of about 20 pintails off the mouth of Savanoski River on August 21. The same day, Schaller saw more pintails among large flocks of waterfowl that flew eastward high over Iliuk Arm.

All 1940 observations of pintails were made only during the period

September 7 (approximately) to 24. Thus the species appears to be a late August–September migrant in the Katmai area. It also seems to be limited to the lakes and larger rivers at low altitudes west of the Aleutian Range. At no time was the pintail observed on Shelikof Strait or the bays thereof. The species was found in association with other waterfowl, particularly the mallard.

Anas carolinensis Gmelin, green-winged teal. The species occurred in small numbers on rivers and ponds, chiefly west of the Aleutian Range. However, a group of four teals was seen July 25, 1953, on a small pond near the mouth of Alagogshak Creek, which empties into Katmai Bay on Shelikof Strait.

The largest aggregations of teals which we found were on Brooks River (where a flock of 12 was seen August 24, 1954) and in the marshes at the western end of Lake Coville. These marshes, with the lower portion of American Creek, formed the optimum area in the Monument for the species. Robert Luntz and I found a considerable number of teals there on September 2, 1953. The following year, on July 18, Schaller and I flushed a female with 11 well-developed but still downy young near the mouth of American Creek.

Messrs. Robert Johnsrud and Ronald Kistler, assistants to geologist Werner Juhle during the first season of the Katmai Project, recorded the presence of two groups of ducks on August 18 at an elevation of "nearly 1,000 feet" on Margot Creek. The stream at this altitude was small; it was located between Mount Katolinat and Mount Martin, and closer to the former. The groups contained two and eight birds, respectively. Johnsrud and Kistler did not identify the ducks. However, because of the agility needed for landing and taking off from these small water areas, and because the teal is the only waterfowl that has been known to use water areas at this or higher altitudes in Katmai National Monument, it is likely that the birds were green-winged teals. This information was given to me orally by Johnsrud who referred to notes of the occurrence made the same day, August 18, 1953.

A highly unusual occurrence was recorded about August 15, 1954, by Garniss Curtis. On the beautiful pond ("Fissure Lake") at the foot of the northwestern glacier on Mount Mageik, at the head of the River Lethe, he saw a flock of about 16 waterfowl which apparently were green-winged teals. The elevation of the pond was 2,200 feet and the area was completely barren of vegetation. About 200 yards away, on the tuff which covered the valley floor, he found the partially eaten carcass of a teal. The flesh was still damp and bright red, so

the carcass must have been torn open only a short time previously. As far as is known, the only mammalian predators that come even rarely into this barren valley are bear and wolf. However, winged predators, such as bald eagle, raven, and perhaps peregrine falcon and golden eagle are also possibilities, particularly if the duck had been sick or disabled. Later the same day, Curtis saw a bird at nearby Mount Cerberus which he tentatively identified as a peregrine, and about a month earlier he obtained a good view of a golden eagle as it flew across the western slope of Katmai Volcano.

Marcca americana (Gmelin), American widgeon. I did not personally observe this species in the Monument. However, two widgeons were seen by Schaller on July 18, 1954, as they were swimming in a small, marshy pond near American Creek a couple of miles above its outlet. This point was close to—perhaps actually outside of—the northern boundary of the Monument. Hine (1919, p. 479), in the summer of 1917, saw widgeons occasionally in the Katmai Bay region, and obtained several specimens from small ponds near the mouth of Katmai River.

Apparently the species is confined to fresh water and is scarce or locally distributed in the region.

Spatula clypeata (Linnaeus), shoveller. The sole record of this duck in Katmai National Monument is based on a sight observation by me of one bird in Brooks River, September 7, 1940. Conditions were favorable at the time for identification of a distinctive species with which I am familiar elsewhere.

Aythya marila nearctica Stejneger, greater scaup (race presumed). The scaup was a fall migrant in the Katmai area, arriving about the first of September. Only two exceptions appear in the field record. The first consists of two birds, apparently a pair, that I saw on July 16, 1953, in a little cove on the south shore of Naknek Lake about a mile north of Brooks River. A second observation was made by Schaller, July 13, 1954. On a small pond between Coville River and the North Arm of Naknek Lake, he saw two pairs of scaups which were accompanied by three and five young, respectively.

Scaups appeared in numbers on August 30, 1953, along the Bering Sea slope. I saw them frequently for the next 10 days, notably in Research Bay on the south shore of Iliuk Arm, on Lake Coville, on the western portion of Brooks Lake, and along Headwaters Creek.

In this region, my one record of scaups in 1940 was made September 9 at Brooks Lake where these ducks were common. Later that year, on October 4, I saw several flocks of scaups between Katmai and Amalik Bays on the Shelikof Strait coast.

Bucephala islandica (Gmelin), Barrow's golden-eye (species presumed). During the 1954 season this was one of the more plentiful ducks on fresh water in the Monument. We saw golden-eyes at frequent intervals throughout July and August, although usually in small numbers—single birds or twos and threes. However, the circular pond about a quarter of a mile east of the mouth of Brooks River was a favored place, where Brody and I saw at least 20 and as many as 34 golden-eyes on successive days throughout the last two weeks of August. All were females and juveniles. Schaller recorded broods of three young July 4 on Grosvenor Lake; three July 24 on the same lake; and a single young August 2 in Iliuk Arm. I saw a female with eight young July 31 on the small lake a quarter of a mile east of Brooks River, and another with two young August 2 at a beaver pond on the north shore of Iliuk Arm about 2 miles west of the outlet of the Savanoski River.

In the lakes region of the Monument, golden-eyes were scarce during September of 1940 and 1953. I saw them only once each season, on the 9th and 10th respectively, and both times on Brooks River. However, the species was abundant October 5 and 7, 1940, in Amalik, Kafia, and Kukak Bays. On the former date I also saw hundreds of golden-eyes resting on the extensive mud flat at the head of Geographic Harbor.

Hine (1919, p. 480) concluded that the species was rather common in the Katmai Bay region during the summer of 1917. He collected a specimen on August 20 from "a small lake," presumably in the lower Katmai River valley.

Histrionicus histrionicus (Linnaeus), harlequin duck. We found that harlequins were scarce throughout Katmai Monument during the summer months. I recorded a female with seven small ducklings at the circular pond a quarter of a mile east of the mouth of Brooks River on July 15, 1953, and three birds (possibly a female with two large juveniles) near the mouth of a stream flowing into the head of Kukak Bay on August 6, 1953. Schaller saw two harlequins in eclipse plumage on a sand bar in Brooks River, July 26, 1954. Both sexes were seen by Gabrielson flying near the falls on the same stream, July

19, 1940. On that date he collected a male harlequin at Brooks Lake. (Gabrielson and Lincoln, 1959, p. 207.)

Polysticta stelleri (Pallas), Steller's eider. Within the Monument my only records of Steller's eider were made in 1940. A flock of six was seen on October 4 in Amalik Bay and the same or another similar group on the following day. Several lone birds were observed southward along the coast as far as Katmai Bay. The species appears to come into the area as a late fall migrant.

Somateria spectabilis (Linnaeus), king eider. Hine (1919, p. 480) shot specimens near the mouth of Katmai River, June 25, 1917. He believed that many of the hundreds of ducks that were fishing far out on Katmai Bay at the time were of this species. I did not record it during any of my field trips in the Monument.

Melanitta deglandi (Bonaparte), white-winged scoter. While most abundant on the bays and coast of Shelikof Strait, white-winged scoters were fairly numerous at times on inland waters. I did not observe them at all in the latter habitat during the summer of 1953 or fall of 1940, but saw them frequently from July 6 to August 25, 1954. Flocks of 20 to 50 birds flew between Coville and Grosvenor Lakes, passing over our camp on the connecting stream, on several occasions in July. We also saw six or eight scoters on the small lake near the portage trail between Lake Coville and the Bay of Islands, July 17. I found a flock of eight birds, and a female with one juvenile young, on the pond east of the mouth of Brooks River, July 31. Brody saw seven fully plumaged adults (three drakes and four hens) at the same pond on August 24. Small groups and individuals were seen at intervals during August on Naknek Lake, the North Arm and Iliuk Arm.

Schaller recorded several large flocks of white-winged scoters along the coast on July 11, 1954. I saw the species at intervals during July-August, 1953, in Kukak Bay and on July 28 in Amalik Bay. The following day, large rafts of birds were congregated off Cape Douglas. I found scoters very numerous on Shelikof Strait during the first half of October, 1940. They were "abundant to very abundant" along the entire mainland coast from Katmai Bay to Cape Nukshak.

Melanitta perspicillata (Linnaeus), surf scoter. In the Katmai area, the species is practically limited to marine coastal waters. Within the Monument I have observed it only October 4 to 7, 1940, when it was

"abundant" from Katmai to Amalik Bays and in Kafia and Kukak Bays, and "common" in Kinak Bay. Elsewhere in the region we saw five surf scoters August 26, 1954, at the mouth of McNeil River on Kamishak Bay, so the species is not entirely absent earlier in the season. However, it certainly becomes much more abundant in late autumn.

The only surf scoter recorded on inland waters within the Monument was a female which was seen by Brody August 30 and 31, 1954, on Brooks River.

Oidemia nigra americana Swainson, common scoter. During summer the species appeared to be absent from inland waters. Even as late as mid-September, 1953, I did not find any common scoters on Naknek Lake, Brooks Lake, or Iliuk Arm. The following year, however, we began to see a few after about August 20. Brody noted small groups, up to four birds, and numerous singles on various parts of Naknek Lake. Schaller recorded one bird August 25 on the North Arm of Naknek Lake.

This scoter was abundant locally on the marine boundary of the Monument throughout the summer and fall, at least during the months covered by my fieldwork there. Two large groups were seen in Dakavak Bay, July 25, 1953; scattered birds were in Amalik Bay July 28, and large rafts of scoters were floating off Cape Douglas on July 29. Later in the season (1940) the species was numerous along the coast from Katmai to Amalik Bays. North of the latter the number decreased until only a few birds were seen in Kafia and Kukak Bays.

Oxyura jamaicensis rubida (Wilson), ruddy duck. Our earliest record was made August 21 (1954), when seven ruddies were seen by Brody and me on Iliuk Arm off the mouth of Margot Creek. They floated quietly in the neighborhood of scattered glaucous-winged gulls, which permitted making an accurate size comparison of the ducks. Luntley and I found ruddies rather numerous on lower American River and in the marshes around its mouth on September 2, 1953. None has been detected in the coastal areas of the Monument. Judging from the lateness of these records, the species is not a summer resident but migrates into or through the area west of the Aleutian Range in late summer and early fall.

According to Gabrielson and Lincoln (1959, p. 239), this species has been recorded in Alaska only once previously, at Kupreanof Island.

Mergus merganser americanus Cassin, common merganser. Gabrielson saw a bird on Brooks Lake, July 9, 1946, the only record for the species within the Monument. (Gabrielson and Lincoln, 1959, p. 244.) Osgood (1904, p. 55) also identified one adult male among ducks killed by natives on Becharof Lake during the first two weeks of October, 1902; this was a dozen miles west of the present Monument boundary, but in a similar environment ecologically. I recorded the species (September 4, 1940) only on the Naknek River, which is more distant and faunistically rather distinct from our area.

Mergus serrator serrator Linnaeus, red-breasted merganser. This is the most common and widespread waterfowl in Katmai National Monument, and the most abundant duck on the lakes and streams of the interior. Of the many days that we spent in boats or hiking along river banks, few passed without the sighting of at least one "fish-duck." The species was so common and ubiquitous that ordinarily only unusual numbers or other circumstances concerning it were recorded in field notes.

Waters where mergansers were most abundant included the North Arm of Naknek Lake, eastern Lake Coville and western Grosvenor Lake, Brooks Lake, Brooks River, Coville River, American Creek, and the marsh at the western end of Lake Coville. Coville River was particularly notable for mergansers, which fed at the outlet into Grosvenor Lake. On September 2, 1953, I counted 40 birds fishing here at one time, and was unable to complete the tally because of their rapid movements. Brooks River likewise was popular with the species, but it never attracted such large numbers as Coville River.

Mergansers were present also in the bays along Shelikof Strait but were comparatively few. (I termed it "common" only in Amalik Bay early in October, 1940.) This scarcity was especially evident during July and August when the young were too small to cope with the rough water that prevailed at times on the larger bays. Broods in this region were generally in or near sheltered coves or at the mouths of streams to which they could retreat in case of need. The total altitudinal range of the waters on which mergansers were seen was sea level to 500 feet.

A nest containing 13 eggs was found July 9, 1954, on the western tip of a small island in central Lake Coville near the south shore. It was about 8 feet above and 10 to 12 feet distant from the water. The nest was a foot or so from the edge of a little bluff which had been eroded by storms and dropped to the sloping gravel beach. Dense grass

on the top of the bank gave complete concealment in all directions. Two well-beaten paths led from the nest to the edge of the bluff, from which the female merganser could launch into flight without walking to water. The paths were only a foot or two in length and were practically tunnels in the thick grass which closed together overhead. Grass was pulled across the openings so that even from the beach the area appeared undisturbed. Wind apparently covered the sound of our approach, and I was only a few feet away when the brooding female sprang through the grass into flight without attempting to cover the eggs.

The number of young in the various broods recorded were as follows: 3, June 30; 15, July 5; 4, July 13; 7, July 16; 23, July 17; 2, July 26; 8, August 5; 11, September 8. Many other broods were seen but the young were not counted. The variation in the size of the young mergansers throughout the summer was notable. I recorded "large" ducklings as early as June 30 and small ones, still downy, as late as July 26. Gabrielson saw "numerous broods" on Brooks Lake, July 19, 1940, but did not mention the development stage of the young. (Gabrielson and Lincoln, 1959, p. 248.)

Red-breasted mergansers were seen throughout both field seasons of the Katmai Project. They were recorded as early as June 29, 1953, and as late as the end of my fieldwork, October 7, 1940. In the 1954 season the species seemed to become less abundant after the first of August. However, somewhat the reverse trend had occurred during the preceding year.

Iline (1919, p. 475) in 1917 found the red-breasted merganser common in the Katmai Bay area.

Accipiter gentilis atricapillus (Wilson), goshawk. A total of six goshawks were counted for the entire period of the Katmai Project. All were seen in the western portion of the Monument from August 25 to September 5, 1954. This peculiar grouping of records suggests that a migration "wave" was in progress.

A lone immature goshawk was seen over the north part of the Bay of Islands, August 25, and another over eastern Brooks Lake, August 31. Fully adult birds were noted on the tundra, at about 1,500 feet elevation, 2 or 3 miles north of Idavain Lake on August 29, and in the spruce forest near the outlet of Brooks Lake on September 1. Two goshawks of undetermined age hunted over the tundra south of Contact Creek and about 6 miles above the latter's junction with Takayoto Creek on September 5. The altitudinal range of the 6 localities is 40 to 1,500 feet.

The bird seen north of Idavain Lake was a beautiful pearly gray male. As we watched, it swooped into a great flock of pipits and passed through without making a catch. Then the pipits veered and chased the goshawk as the latter flew off out of sight over a ridge.

The second adult goshawk came flying slowly over the spruce forest near the outlet of Brooks Lake and perched on the top of a tree about 75 feet from the path where I was walking. I stopped to watch the bird, which sat still, except for turning its head, for about five minutes. Then it flew off. It is possible that the goshawk's attention was caught and held by the carcass of a kittiwake that I had found dead on the shore of Brooks Lake and was carrying to camp for use as a museum skin.

Accipiter striatus velox (Wilson), northern sharp-shinned hawk. A sharp-shinned hawk darted overhead on the morning of September 9, 1953, as I was eating breakfast in a grove of spruces at the mouth of Headwaters Creek. The bird alighted on a piece of driftwood on the shore of Brooks Lake a hundred yards north of the Creek. After perching there for about 5 minutes, it resumed its flight and disappeared. This was the only sharp-shin recorded in the Monument.

Buteo lagopus s. johannis (Gmelin), American rough-legged hawk. A melanistic rough-leg was observed sitting on an open slope above the south shore of upper Kukak Bay on the late afternoon of August 6, 1953. After a short time the bird took to the air and circled the hill repeatedly, calling as it hunted for food. The following year, on July 5, Schaller and I found a pair of rough-legs on the north shore of Grosvenor Lake about 3 miles northeast of Coville River. The birds had a nest in a shallow cave high up on the face of a cliff which rose vertically from deep water. As we lacked ropes, a closer examination was not possible. Later that day we saw a rough-leg, which may well have been one of the pair, hunting over the slopes just south of Coville River. Brody and Schaller found a fine adult in a dead spruce near the mouth of Savanoski River, August 21, 1954, and Schaller sighted another lone bird flying over the tundra north of Idavain Lake at about 1,500 feet elevation on August 29, 1954.

A concentration of rough-legged hawks occurred September 14-17, 1940, near Three Forks at 600 feet elevation in the lower end of the Valley of Ten Thousand Smokes. While some of the observations may have represented duplicate individuals, I saw five birds hunting at one time in a loose group. The hawks probably were migrating.

Aquila chrysaëtos canadensis (Linnaeus), golden eagle. While typically a bird of the interior mountains, the golden eagle occurs in Katmai National Monument at rare intervals. I saw two birds, not fully mature, perched on a rocky bluff at about 1,500 feet elevation between Idavain Lake and the North Arm of Naknek Lake on August 17, 1953. A year later, on August 21, Brody and I watched with binoculars a bird of prey that circled among the crags near the southern summit of Mount LaGorce, and which by its actions and flight may have been a golden eagle.

Dr. Garniss Curtis reported (personal communication of April 7, 1955) an eagle that flew past him about noon of July 4, 1954, as he stood on the west slope of Mount Katmai. The elevation was about 5,000 feet. The bird came in a steep glide from the direction of the south notch in the crater rim. It passed so close overhead that Curtis was able to see the frayed ends of the primaries and the rather emaciated body, as well as "lightish patches" on the wings. He stated, "I have watched Golden Eagles of all ages many times (in the Sierra Nevada of California) and mature Bald Eagles on a few occasions, and I would say that in the manner of flight and general appearance he (the bird described above) was a Golden Eagle."

Haliaeetus leucocephalus alascanus Townsend, northern bald eagle. The bald eagle is a common and conspicuous member of the avifauna. It may have been a little less numerous in 1953-1954 than during my first visit to Katmai in 1940. However, the difference, if any, had no real significance except as evidence of normal fluctuations to which all animals are subject. In any event, eagles seem to have been much more abundant during recent years than at the opening of the twentieth century. In 1902, when W. H. Osgood spent a month on the Alaska Peninsula not far southwest of the present Monument, he saw only one eagle in a month's time. We saw eagles almost daily, or at least several times weekly, during our field study.

The species was mentioned in my field notes on 16 occasions during 1953, from June 29 to September 9, and 13 times in 1954, July 5 to August 31. This is not a complete record, however, for birds were seen on numerous other occasions. In 1940 I noted eagles many times throughout my stay in the area, from September 5 to October 9.

Bald eagles could be expected almost anywhere on the lakes and larger streams west of the Aleutian Range, and along bays and headlands as well as on the lower courses of the rivers emptying into Shelikof Strait. Most of the birds occurred at altitudes of 50 to 500

feet. The presence of spawning and dying salmon anywhere was assurance that scavengers—eagles, ravens, and magpies—would gather to feed or to search for food. In mid-September, 1940, I saw several eagles in the upper Ukak Valley and along lower Windy Creek at elevations of 600 and 1,000 feet, respectively. Hine (1919, p. 475) reported the species flying over the Valley of Ten Thousand Smokes, 1,000 to 2,000 feet above sea level, during the summer of 1917. However, the lakes and larger streams of the Bering Sea plain and the coastline of Shelikof Strait were the normal habitats of the species.

Nests, either occupied or in usable condition, were seen at the following points in 1953: At least two west of the cannery on the south shore of Kukak Bay; one near the south shore of the north prong of Kukak Bay; two near the western foot of Mount Pedmar; and one on the northeastern cliffs of Mount Pedmar. A nest in each of the following localities was recorded in 1954: north shore of Lake Coville; north shore of Grosvenor Lake; about 2 miles north of Coville River, and about a mile west of the portage between Lake Coville and Bay of Islands. The last two nests were found and reported by Schaller. Six of the structures found in 1953-1954 were built on rock columns, one on the ledge in the face of a cliff, and four in trees.

The youngest eaglet seen, which was estimated to be two or three days old and covered with dirty-grayish down, was examined by Schaller on July 7, 1954, at the aerie on the north shore of Lake Coville. The previous year I saw two large, fully feathered young, July 28, in the nest on the cliffs of Mount Pedmar, and two more, August 5, at a similar stage of advancement in the north prong of Kukak Bay. During both years I saw only three immature bald eagles which had left the nest, and Schaller saw another which was almost invariably accompanied by an adult. One of the young eagles seen by me was apparently disabled or not yet capable of flight. When watched from the helicopter on August 4, 1953, it was walking and threshing about in the sedges of the marsh in Swikshak Lagoon.

The peculiarity of the rock structure in numerous places along the coast, especially in Kukak Bay and at Mount Pedmar, facilitated the formation of rock columns through erosion. A number of these structures offered excellent nesting sites which were unscalable by four-footed predators. However, some of the nests could be reached by agile humans, and some depredations on eggs and nestlings undoubtedly occurred. In the summer of 1953 a portion of the Army Engineers Company doing topographic mapping in the Monument was based on Kukak Bay. As a diversion, some of the men took an

eaglet from a nest and attempted to rear it. Tiring of it shortly, the men placed their "mascot" in another nest which was occupied by a single eaglet. We were informed that the parents of the latter killed and ate the intruding young bird.

Some shooting of eagles undoubtedly occurred, especially along the coast of the Monument where commercial fishermen netted salmon and took refuge from storms during the summer months. However, the species seemed to be maintaining itself and the population could be termed "satisfactory."

Circus cyaneus hudsonius (Linnaeus), marsh hawk. This harrier was rather scarce but widely distributed west of the Aleutian Range. During the two field seasons of the Katmai Project, I made 11 observations of single birds at the following points: Lower Savanoski River (twice); north base of Mount Katolinat; mouth of Margot Creek; lower Brooks River; Contact Creek 6 miles above its junction with Takayoto Creek; north of Idavain Lake; Coville River; mouth of American Creek (twice); and east of Murray Lake (about a mile north of the Monument boundary). In addition, Schaller saw a bird on the north side of Lake Coville and another high on Mount Dumpling. Also, Brody recorded a second individual, not seen by me, north of Idavain Lake.

My observations of marsh hawks in the fall of 1940 were made at Brooks River outlet; mouth of Ukak River; lower end of Valley of Ten Thousand Smokes, and site of Katmai Village. The latter is in the lower Katmai River valley about 2 miles from Shelikof Strait, and is the only place in the Monument where the species has been recorded east of the Aleutian Range.

The marsh hawks that were seen obviously hunting (as opposed to traveling from one locality to another) were over marshes (5), rank grassland (3), and tundra (6 instances). The great majority of the areas were below 500 feet in elevation, but 3 were at 1,500 feet or higher. The upper limit of the species, as indicated by our actual sight records, was 2,050 feet.

My earliest observation of the marsh hawk was July 6 (1954) and the latest October 4 (1940). All except 1 of our collective 20 records were made after mid-July, and all except 4 were made later than the middle of August.

Pandion haliaetus carolinensis (Gmelin), osprey. In view of the plentiful fish supply and extensive area of fishery waters, this bird

was less numerous than could be expected. I recorded it four times in 1954, July 18 to August 25; on seven occasions in 1953, July 24 to September 8; and only once in 1940, on September 7.

The lower reaches of Katmai River and Alagogshak Creek provided the most favorable locality for ospreys. I saw several birds on Katmai River and two on Alagogshak Creek on the same day, July 25, 1953. The previous day I also sighted or heard at least two ospreys on an alder-covered ridge in Geographic Harbor. The abundant supply of trout in Brooks River was an attraction and I saw an osprey there at least once each season in 1940 and 1954. Gabrielson recorded a single osprey at Brooks Lake, July 19, 1940, and another July 9, 1946. Gabrielson and Lincoln (1959, p. 278) declared, however, "There are more fish hawks about Bristol Bay and the lakes at the heads of the tributary streams at the present time than in any other part of the State."

I watched a lone bird August 20, 1953, as it flew slowly along above a small stream on the great delta of the Ukak River. The following year, on August 2, we found a nest in a drowned spruce that stood well out in the Ukak itself. An adult osprey guarded it. We were unable to see into the nest from a distance, or to approach it owing to the rushing stream and extensive flats of quicksand.

Single ospreys were noted also at Coville River around mid-July, 1954; on lower American Creek, July 18, 1954; over the north portion of the Bay of Islands, August 25, 1954; on the northern shore of Lake Coville, September 2, 1953; and (possibly two birds) on Headwaters Creek, September 8, 1953.

An osprey on Headwaters Creek about $1\frac{1}{2}$ miles (air line) west of Brooks Lake was watched on the evening of September 8, 1953. The bird sat in the top of a spruce and scolded vigorously as a northwestern shrike made repeated passes at it. However, the osprey did not attempt to take punitive action.

Falco rusticolus obsoletus Gmelin, gyrfalcon. Schaller identified this species on the rolling tundra with many ponds south of Angle Creek and about 6 miles upstream from the latter's junction with Takayoto Creek. He described the circumstances as follows: "Three gyrfalcons, all of the dark color phase, dived and dodged low over the alder brush on September 5, 1954. All three pursued and worried a short-eared owl, which after a hard chase finally eluded its tormentors."

This is the only recorded instance of the occurrence of gyrfalcons

within Katmai National Monument. Several birds were seen by Osgood at Becharof Lake on October 4, 1902, and Brody saw the species near Naknek on two occasions during the summer of 1954. These habitats are quite similar to that of the Angle Creek area where our birds were recorded, and about 11 miles and 32 miles, respectively, west of the western boundary of the Monument.

Falco peregrinus pealei Ridgway, Peale's peregrine. The species is included in this list of Monument birds on the basis of a report by A. Samuel Keller, petroleum geologist of the U. S. Geological Survey, who made field investigations in the area during the summer of 1954. He was familiar with the peregrine through experience in the Brooks Range of northeastern Alaska, where the species is relatively abundant.

Mr. Keller saw two peregrines on July 22, 1954, at a rock bluff that arose from the south shore of Grosvenor Lake about 2 miles east of the portage between that lake and the Bay of Islands.

Dr. Garniss Curtis reported seeing a bird, which he tentatively identified as a peregrine falcon, near Mount Cerberus on August 13, 1954. Only a distant view was obtained, but Curtis was certain that the bird was not a pigeon hawk—the most likely alternative in the region.

Falco columbarius bendirci Swann, western pigeon hawk. We recorded pigeon hawks on six occasions from July 8 to August 31, 1954, and the occurrence record is extended into the fall by observations on September 9 and 16, 1940. The species was not seen at all during the 1953 season.

Schaller and I on July 8, 1954, watched two pigeon hawks attacking a pair of large hawks (which we were unable to identify with certainty, but which resembled Swainson's hawk). The larger birds had a nest containing four young on a shelf high up in the southeastern cliff of the largest island in the eastern part of Lake Coville. As we approached by boat, the parents took to the air and circled over us screaming loudly. Two pigeon hawks appeared suddenly from over the island and engaged in an aerial "dog-fight" with the bigger species. Whenever one of the large hawks was closely pressed, it would turn over and strike with its talons, and the falcon would sheer off. After several minutes the pigeon hawks retired. Circling the island, we saw one of them perched in a spruce tree tearing at a piece of food which we were unable to identify even in a general way. If the pigeon hawks

had a nest on the island, as seemed possible from their aggressive behavior, we did not see it.

One of the Lake Coville birds was seen again at the same island on July 16. I recorded other lone pigeon hawks flying high across Iliuk Arm August 21, on the south shore of the North Arm of Naknek Lake August 25, and at the mouth of Brooks River August 31. Schaller also saw a single bird near the last-named locality on August 24. My 1940 records consisted of single birds on the lower Ukak River September 9 and on Windy Creek above Three Forks on the 16th. Hine saw the species commonly in the region of Katmai Bay during the summer of 1917. The altitudinal range of these localities is approximately 40 feet to nearly 1,000 feet.

We did not see any young of the species. Hine (1919, p. 482), however, recorded four juveniles accompanied by two adults in flight over the south side of Katmai Bay about August 1, 1917.

The pigeon hawk that we observed August 25, 1954, at the south shore of the North Arm of Naknek Lake was diving aggressively at a group of magpies and glaucous-winged gulls. These birds had congregated to feed on dead salmon at the mouth of a small stream flowing off the north slope of Mount LaGorce. The magpies and gulls ignored the hawk which finally flew off. Hine (1919, p. 483), however, recorded an incident which may indicate that the tables may be turned in this relationship. On August 15, 1917, at Cape Kubugakli (south side of Kashvik Bay, and the southwestern corner of the Monument), he found a magpie attacking a pigeon hawk. Six other magpies were nearby, and Hine considered that they also had been engaged in the encounter. The hawk was so severely injured that it was unable to fly and allowed the man to walk up to it.

Falco sparverius sparverius Linnaeus, northern sparrow hawk. The sole sparrow hawk record for the Monument came from the northeastern shore of Lake Coville. On September 2, 1953, I watched one of these little falcons as it chased two magpies among scattered spruces and cottonwoods. The "attack" appeared to be more playful than serious and the magpies hopped slowly from one spruce to another only when the hawk became unduly persistent.

The following day, September 3, I saw two more sparrow hawks, but these birds were well outside of the Monument. The first hawk made an unsuccessful stoop at a sparrow-size bird in a cottonwood grove at the junction of the South Fork with the main stream of Kamishak River. The locality was 325 feet above sea level and about

16 miles north of the Monument boundary. The other sparrow hawk was also in a cottonwood grove, which was on upper Kamishak River at an elevation of 750 feet about 11 miles from the Monument line.

Canachites canadensis osgoodi Bishop, Alaska spruce grouse. The species was fairly numerous in its chosen habitat, spruce or mixed spruce-deciduous forest, west of the Aleutian Range. No trace of it was found east of the mountains, even in the old spruce forest on the flats back of Hallo Bay. Evidently this and the smaller bits of spruce woods along Shelikof Strait were so isolated that the grouse had not been able to bridge the gap of treeless mountains and snowfields.

Spruce grouse had a very limited distribution in altitude within the Monument. All those seen were below the 200-foot contour. The total vertical range, therefore, was less than 150 feet.

Spruce grouse were recorded in September 1940 at the north base of Mount Katolinat in the angle between Ukak River and Iliuk Arm. There the species was abundant and as many as five birds were seen at one time.

During the summer of 1953 grouse were found more sparsely: Two birds flushed and droppings abundant in a spruce grove on the north shore of Naknek Lake 2 to 3 miles northwest of the Narrows, July 7; a female with one large young on the spruce-alder dune west of Old Savanoski, July 17; a fine male at a spruce-bordered bog about 3 miles southwest of Coville River, August 17; and one bird of undetermined sex in mixed spruce-cottonwoods near our camp on Savanoski River, August 24.

Schaller located five broods of grouse in stands of spruce around Lake Coville between July 5 and 15, 1954. The young, all able to fly, numbered three, four, five, five, and six, respectively. During the rest of the season we found the species only in the nearly pure spruce forest east of Brooks River and Brooks Lake. Two birds were reported August 19 by Schaller and two more on the same day by Mrs. John Walatka, comanager of the public camp, from the woods between Brooks River Falls and the fisheries laboratory at the outlet of Brooks Lake. Brody and I found two birds, August 31, about 300 yards apart one-half mile east of Brooks Lake. These grouse were wary, springing into the tops of spruces when flushed and watching sharply as we approached. They allowed us to walk to within 30 to 50 feet, then shot off like rockets for flights of 250 or 300 feet. After two or three such movements, each bird became even more alarmed and flew off much farther to evade us completely. I found one more grouse in 1954, near Brooks River Falls on September 1.

Lagopus lagopus alexandrae Grinnell, willow ptarmigan. It is sometimes difficult to distinguish this species from the rock ptarmigan under summer field conditions, particularly in the case of females. The plumage of the willow ptarmigan is generally more rusty and the alarm cackle is higher pitched and harsher than that of the rock ptarmigan. The color of the latter, at least in the Katmai region, is distinctly gray rather than brown. To some extent, the two species share the same habitat, but the willow ptarmigan prefers the lower elevations and a mixed alder-willow-tall grass type of vegetation. (Pl. 4, fig. 1.)

The rock ptarmigan occasionally may be found in the upper fringe of this type, but its principal range is the windswept tundra where the grasses are only a few inches tall and the woody plants are dwarf birch, dwarf willow, and patches of alders in the shelter of ravines and hollows. (Pl. 4, fig. 2.) In Katmai Monument west of the Aleutian Range, the line of demarcation between these two vegetation types, and between the ranges of willow and rock ptarmigans, is approximately 1,000 feet. On Mount Dumpling the types merge about 200 feet higher; in the mountains north of Lake Grosvenor the junction may be nearer 800 feet elevation. The milder climate of the eastern slope, due to warmer, more humid air from the Pacific Ocean, permitted the willow ptarmigan habitat to ascend to about 1,500 feet above sea level. These habitat boundaries, of course, are only approximate; one type merges gradually into the other and both are affected by slope and exposure to sun and wind.

Altitudinally, the willow ptarmigan's range overlaps that of the spruce grouse. However, the latter is closely associated with the spruce forest while the ptarmigan is a bird of more open areas with deciduous thickets. The white wings of the ptarmigan serve to distinguish it at all times from its woodland relative.

During the period of the Katmai Project willow ptarmigans seemed to be increasing in population. They were not plentiful in 1953, when I recorded birds as follows: Two adults and eight young about the size of a full-grown bob-white quail at the head of Kukak Bay, July 25; at least four birds, Cape Douglas, July 29; one on the portage between the Bay of Islands and Grosvenor Lake, September 1; one between Hammersley Lake and Murray Lake, September 5; and two kills (clusters of feathers) on the moraine near Headwaters Creek, a mile west of Brooks Lake, September 8. Also, three adults (two of which were accompanied by seven and three young, respectively) and one predator kill on the eastern spur of Mount Dumpling, July 11, 1953, probably belonged to this species.

The following year, I recorded (presumed) ptarmigan sign on the ridge south of Lake Coville, July 9, and abundant sign near the outlet of the largest stream flowing off the north slope of Mount Katolinat, August 21. (A. Samuel Keller of the U. S. Geological Survey informed me that he had flushed a number of ptarmigans in this area a week or so previously.) Brody and I saw a flock of 13 willow ptarmigans on the slopes north of Idavain Lake on August 29, and Schaller separately counted more than 30 birds in the same general area. Fourteen of these, in one group, were mostly males. We tallied at least 45 ptarmigans, in groups ranging from 3 to 15 or more birds, along Contact Creek on September 5. Droppings in this locality were abundant; some were stained blue from the crowberries and blueberries which the birds were eating in quantities.

An unusual occurrence of the willow ptarmigan was recorded when Dr. Garniss Curtis found the remains of a bird about 100 yards south of the junction of the north and south forks of Knife Creek. Here, at an elevation of 2,000 feet, all vegetation had been destroyed by the 1912 eruption and only a few plants had succeeded in reestablishing themselves. Curtis showed the remains (head, part of neck, one entire wing and part of another) to Schaller on August 5, 1954. From the large, heavy beak and red-brown feathers on the head and ruff of the neck, Schaller identified it beyond doubt as a willow ptarmigan.

The species was not as abundant in 1940, when I was told by persons at Naknek that it was recovering from a point of extreme scarcity. I saw a total of 3 flocks of 15 to 25 birds each, September 27 and 29, on the north slope of Mount Dumpling and thence to the western boundary of the Monument. From a distance, all these birds appeared to be pure white, having changed into the full winter plumage. Many of the birds that I saw near Contact Creek on September 5, 1954, were in the very early stage of the seasonal change. Others showed no appreciable signs of white on the body.

Lagopus mutus nelsoni Stejneger, Nelson's rock ptarmigan. Distinguishing field characteristics and local habitat preferences of this species are described in the first paragraph under "willow ptarmigan" (p. 109).

Many signs of rock ptarmigans were seen on the upper 500 feet of Mount Dumpling during my two trips there, July 10 and August 17, 1953. On the former date I found a pair with four young, an adult with two young, and an adult with a single youngster. One grown bird was unaccompanied. The environment was high-altitude grassland,

with a few low alders and spruces in protected depressions. Many signs, but no birds, were also observed on the tundra at 2,000 feet elevation about 2 miles northeast of Idavain Lake on August 17, 1953. The principal plants were grasses, crowberry, blueberry, and dwarf willow.

Johnsrud and Kistler reported seeing an adult and four young ptarmigans (undoubtedly of this species) in a "grassy area" at 2,200 feet elevation on the headwaters of Kejulik River (south slope of Mount Martin) on July 24, 1953. Nearly a month later, on August 18, Johnsrud scared up a flock of at least 30 birds southeast of Margot Creek and northeast of Yori Pass at an elevation of 1,800 feet. Because of the elevation and tundra environment, it is fairly certain that these birds were rock ptarmigans rather than willow ptarmigans.

Brody and I found a flock of six as well as several lone birds on August 29, 1954, north of Idavain Lake between 1,200 and 2,000 feet above sea level. The group of six ptarmigans was on and near the edge of a rock slide. American pipits and Alaska longspurs were extremely abundant roundabout. On the same day, during a 6-hour walk in this general area, Schaller counted over 150 rock ptarmigans, including one flock of about 40. This locality was 3 to 5 miles west of the site of my second observation of the rock ptarmigan on August 17, 1953 (above).

Hine (1919, p. 482) saw only one rock ptarmigan in the Katmai Bay region, and shot the bird for a museum specimen. It was "on the mountain side just back from Kashvik Bay, August 23, 1917." He did not give the elevation of the area. My own data indicate that the species ranges from 1,200 to 2,200 feet in altitude.

Haematopus bachmani Audubon, black oystercatcher. This species was scarce—or perhaps local in occurrence—within Katmai National Monument. We recorded it only three times, twice in 1953 and once the following year. All occurrences were on salt water.

I saw two oystercatchers on a rock dike at Cape Douglas, August 29, 1953. Two others were standing in a flock of glaucous-winged gulls that were resting on the gravel near the large creek or river which empties into upper Kukak Bay north of Aguchik Island, August 6, 1953. A lone bird was observed by Schaller in Kuliak Bay on July 11, 1954. It flew past him as he stood on the rocky peninsula that juts into the bay and divides its head into two coves.

Charadrius semipalmatus Bonaparte, semipalmated plover. This little plover was not common at Katmai. I recorded the species on

only four occasions: Two birds at the mouth of Headwaters Creek, June 30, 1953; three birds on the north shore of outer Kukak Bay, August 2, 1953; four birds at the mouth of American Creek, July 18, 1954; and a single bird at the mouth of Ukak River, August 2, 1954. In two instances, the birds were on mud flats at the outlet of streams; in one case on a gravel or stony marine beach, and in the fourth instance, on a fine sand beach of an inland lake. All the birds were at low elevations—sea level to about 200 feet. The seasonal grouping of the observations—June 30 to August 2—is not significant owing to the paucity of the records.

The actions of the two birds that were seen June 30 near the outlet of Headwaters Creek, coupled with the sandy beach environment, strongly suggested that eggs or young were in the vicinity.

Pluvialis dominica fulva (Gmelin), Pacific golden plover. My sole record of this species was made at our Savanoski camp site, where a lone golden plover dabbled and probed for insects in the mud and shallows of the little creek for several hours on August 20, 1953. (Pl. 12, fig. 1.) The stream emptied into the Savanoski River a few yards away and was between one-half and 1 mile above the outlet of the latter into Iliuk Arm. The plover was far from shy. It allowed me to make a number of photographs and to watch it at leisure from distances of 16 to 22 feet. The bird was even more indifferent to our mechanic, who was making extensive adjustments on the helicopter which was parked nearby. The plover fed casually within 50 feet and did not move when the mechanic, feigning ignorance of its presence, walked by several times only 5 feet away.

Hine (1919, p. 482) observed a number of flocks of golden plovers on the mud flats and sandy areas around Kashvik Bay. He took one specimen, August 24, 1917.

Arenaria interpes interpes (Linnaeus), European turnstone. Gabrielson and Lincoln (1959, p. 338) state, "In migration [this species] is widely distributed . . . Specimens have been taken on Nunivak, September 8, and on Unalaska and Ogliuga Islands in the Aleutians as well as to King Cove and Katmai on the Alaska Peninsula . . ."

The senior author has informed me (in personal communication dated April 10, 1959) that the Katmai specimen was taken August 15, 1917, by James S. Hine. In May 1925 the collector sent the skin for identification to the U. S. National Museum. There it was identified by Harry C. Oberholser as *A. interpes*. As Hine did not mention

the latter species in his list published in 1919, it appears that he failed to recognize it at that time as being distinct from *A. melanocephala*, the black turnstone.

Arenaria melanocephala (Vigors), black turnstone. According to Hine's observations and our own limited data of five records, turnstones migrate through the Katmai region during August. With the exception of one straggler that I saw in Amalik Bay on October 5, 1940, all these birds were seen during the period August 1-19. However, the area is within the breeding range, and further investigation will undoubtedly reveal that the species is a nesting resident. Gabrielson and Lincoln (1959, p. 339) state: "It undoubtedly nests along the shores of Prince William Sound and the Alaska Peninsula, though no actual nests have been found."

In addition to my record cited above, I saw black turnstones on one other occasion on the coast of Shelikof Strait. A flock estimated to number between 30 and 40 birds was observed August 4, 1953, as they flew about and searched for food on the tidal mud flats on the north shore of outer Kukak Bay. The other three sightings were in the western portion of the Monument. I counted 16 black turnstones along about one-quarter mile of the sandy south shore of Naknek Lake north from Brooks River on August 1, 1954, and Schaller saw several (perhaps some of the same birds) near the river outlet on subsequent days. Brody and I found four turnstones, August 17, 1954, on the stony beach of the large island in Naknek Lake on the western boundary of the Monument. The birds allowed us to approach to within 25 feet. Later that day Brody recorded two or more individuals elsewhere on the same island. One bird was seen August 19, 1953, on a mud bar in Savanoski River about a mile below the mouth of Rainbow River. I surmised from its flight course that it might have been moving across the Peninsula from Bristol Bay to Cook Inlet.

Hine found that in 1917 black turnstones "first appeared along the shores of Kashvik Bay about the first of August, and increased in number later. On August 25, flocks of a hundred or more were seen, and at this time it was one of the most abundant shore birds in the locality." (Hine, 1919, p. 482.) He took specimens, which showed some variation in color, August 7 to 21.

Capella gallinago delicata (Ord), Wilson's common snipe. Our records of the Wilson's snipe cover the entire period of fieldwork in Katmai National Monument. The earliest date of observation was

July 7 (1954); the latest, October 5 (1940). I saw snipes, or heard them, on at least 20 occasions during my 3 seasons in the area. Owing, perhaps, to the relative scarcity of habitat, only once was a snipe seen east of the Aleutian Range. This bird was at the head of Geographic Harbor, October 5, 1940. Even at Katmai Bay, however, where marshes were fairly extensive, Hine did not find the species in the summer of 1917.

On the Bering Sea drainage we recorded Wilson's snipes in the following localities: Open marshes and willow swamps around the outlet of Brooks River, where three or four birds were seen on numerous dates in the last two weeks of August, 1954 (by Brody, Schaller, and Cahalane), and on September 5, 1940; sedge marsh 1 mile west of the mouth of Brooks River, two birds seen (one collected by Schiller), July 11 and 13, 1953; sedge marsh east of Research Bay, south shore of Iliuk Arm, two birds, August 30, 1953; marshy shore of island in Naknek Lake on west boundary of the Monument, one or possibly two birds, August 17, 1954; marshes west of lower Ukak River, four birds seen by Been and Cahalane, September 11, 1940; Savanoski Village site, September 13, 1940; upper Ukak River, two birds, September 14, 1940; grassy flat with low willows and alders, north shore of Lake Coville, at least two birds, July 7, 1954; and marshy lagoon back of the north shore of Grosvenor Lake, two birds (Schaller and Cahalane), July 24, 1954. From our camp on Coville River Schaller heard snipes winnowing on several occasions during mid-July, 1954.

Most of the birds were in sedge marshes, either open or with scattered willows and alders, while a few snipes were in deep grass. Two birds (on the upper Ukak River) were found at an elevation of about 500 feet. Otherwise, the species seemed to have a narrow range from sea level to approximately 200 feet elevation.

Actitis macularia (Linnaeus), spotted sandpiper. The species was definitely uncommon in the Katmai region. I saw it once in 1953, on July 12, when a lone bird was noted on the sandy beach of Naknek Lake near the outlet of Brooks River. We obtained five records the following year. On July 5 Schaller and I found two spotted sandpipers on a mud flat at the outlet of a small stream into northwestern Grosvenor Lake. Subsequently, I saw single birds on a mud flat along the northeastern shore of Lake Coville, July 7, and on a gravel bar near a stream outlet at the north shore of Grosvenor Lake, July 12. On the same shore, at a seep in a sand and gravel beach, I found a

female with two juveniles on July 24. The last spotted sandpiper was recorded by Brody, August 17, 1954. This was a single bird on the marshy south shore of the large island in Naknek Lake which is bisected by the western boundary of the Monument.

Tringa solitaria cinnamomea (Brewster), western solitary sandpiper. The species has been recorded only once in or near the Monument. On July 24, 1954, Schaller and I observed four birds in a marshy lagoon back of the north shore of Grosvenor Lake. The place was about 10 miles by air line directly east of Coville River. The solitary sandpipers were foraging in a loose group of least sandpipers and two Wilson's snipes.

Schaller collected one of the solitary sandpipers (his field number 154), a very fat female with small ova.

Heteroscelus incanum (Gmelin), wandering tattler. Hine (1919, pp. 481-482) observed a pair of this species on a rocky section of the coast of Katmai Bay, August 3, 1917. He collected one of them, and obtained another on August 25. The latter was a juvenile bird with white under parts. These appear to be the only records of the wandering tattler for the Monument and vicinity.

Totanus melanoleucus (Gmelin), greater yellow-legs. The visitor to Katmai, whenever he is near marshes or ponds in the nesting season, is rarely out of hearing of the yellow-legs' scream of alarm. The species is present on both sides of the Aleutian Range. I recorded it during late July, 1953, in the coastal lowlands near the mouth of Alagogshak Creek, in the lower Katmai River valley, at the head of Kukak Bay, and (July 11, 1954) on the grassy flats back of the beach dunes in Hallo Bay. Hine, in 1917, saw several pairs along the shore of Katmai Bay and stated (1919, p. 481) that the species nested commonly in that area.

The yellow-legs' habitat was much more extensive in the lake-tundra country west of the mountains and many more observations were made there. Birds were noted on the northern and eastern shores of Lake Coville; at the mouth of American Creek; on the northern shore of Grosvenor Lake; on lower Headwaters Creek; and in the vicinity of the mouth of Brooks River. The latter area was an excellent locality for yellow-legs. A pair was obviously nesting in 1953 at the marsh about 1 mile north of the mouth of the river. The following year a family group of six greater yellow-legs was seen frequently

along lower Brooks River, the adjacent shore of Naknek Lake, and at a circular pond about one-quarter mile east of the river outlet. Gabrielson (Gabrielson and Lincoln, 1959, p. 362) recorded the species on Brooks Lake, at the head of the river, July 19, 1940, and July 9, 1946. The altitude of these places ranged from sea level to about 200 feet.

Yellow-legs were seen by me throughout the summer. The earliest date of observation within the Monument was June 30 (1953); the latest was September 1 (1954). None was found in the area during September-early October, 1940. Apparently the birds leave very soon after the first of September.

The species is closely associated with water or at least marshy ground. The specific habitats and number of bird-unit records made in each within Katmai National Monument are as follows: Creeks or rivers, 16 birds; mud flats, 2 birds; lake shores, 9 birds; marshes, 4 birds; marshy lagoons and marshy ponds, 11 birds; grassy flats, with or without scattered willow-alder thickets, 4 birds. While this tally is haphazard and doubtless includes some duplications of individual birds, it is a rough indication of the yellow-legs' preference for rivers, marshy ponds, and lake shores.

Juveniles were noticed on several occasions. The earliest recorded were on July 24, 1954, when three were seen feeding in a marshy lagoon back of the north shore of Grosvenor Lake. They were capable fliers, but we were able to walk to within 30 feet before they moved away without screaming or showing other signs of alarm.

A yellow-legs was observed August 14, 1954, as it sought small fish in shallow water along the shore of Naknek Lake about 200 yards east of the outlet of Brooks River. The bird waded in quiet water that almost reached its belly. It moved along watching the water and, while within 50 feet of me, snatched up and swallowed two fish that I estimated were 2 inches in length. Considerable difficulty was experienced in swallowing the first fish, but almost none with the second. After each mouthful, the bird rinsed its bill in the water. Dr. Brody also watched a greater yellow-legs feeding on "minnows" in Brooks River, except that this bird was actually swimming while so engaged.

Totanus flavipes (Gmelin), lesser yellow-legs. Except for considerable disparity in size, the lesser yellow-legs is difficult to distinguish from the preceding species. My assistant, Mr. Schaller, who had had opportunity to observe both species near Fairbanks, Alaska, considered that all the yellow-legs he saw in Katmai Monument during

the 1954 season belonged to the smaller kind. However, Dr. Brody was able to compare the two species together on one occasion and felt certain that the large majority were greater yellow-legs. In this instance, a single lesser yellow-legs was with several greater yellow-legs on a bank of Brooks River.

Erolia ptilocnemis couesi (Ridgway), Aleutian rock sandpiper. Hine took three specimens, August 20 to 23, 1917, and stated (1919, p. 480) that only two or three birds were seen by him at any one time along the shore in the region of Katmai Bay. A flock of about 20, however, was found by Osgood October 16, 1902, at Puale Bay, less than 20 miles southwest of Hine's area in the Monument, and specimens were collected.

Erolia bairdii (Coues), Baird's sandpiper. The species was seen only once. I watched a group of four birds probing for food on a sand bar at the edge of the Savanoski River, August 24, 1953. They virtually ignored me as I stood within 50 feet on the low bluff which was the site of the last native settlement of Savanoski Eskimo in the Monument. After about 20 minutes the sandpipers took wing and disappeared far out across the wide river.

Erolia minutilla (Vieillot), least sandpiper. I recorded the least sandpiper on only seven occasions during the entire two seasons of the Katmai Project. In each instance the species was in the well-watered tundra region west of the Aleutian Range at elevations of 50 to 300 feet. Probably by chance, all observations were made in midseason or late season, from July 24 to September 8. More than half of the records, which comprised the great majority of the individual birds, were tallied on one date, July 24, 1954.

On that day we saw five least sandpipers on the sandy beach at the outlet of a creek on the north shore of Grosvenor Lake. A mile east, 4 or 5 of these tiny birds were on a jagged reef that projected 2 to 4 feet above the lake; they seemed indifferent as we passed slowly about 30 feet away in a dory driven by an outboard motor. Proceeding eastward, we found the species numerous at a marshy lagoon behind the north shore of the lake. Associated with it were several solitary sandpipers and a couple of Wilson's snipes. Finally, on the delta of a large stream flowing into Grosvenor Lake we saw about 10 least sandpipers with a female spotted sandpiper and her 2 chicks.

The remaining observations of the species were as follows: A small

group of birds on mud flats west of the Ukak River delta, August 2, 1954; one bird on the sandy beach at the outlet of Brooks River, August 19 and 20, 1954; and an individual on the muddy shore of Headwaters Creek, September 8, 1953. Hine noted a few birds of this species on the beach near the mouth of Katmai River and took one specimen, July 23, 1917.

Schaller collected one of the group of five least sandpipers that we found on the north shore of Grosvenor Lake, July 24, 1954, and assigned his field number 155 to the specimen. It was a male in very fat condition; the testes measured 2×1 , 2×1 mm.

Erolia alpina pacifica (Coues), red-backed sandpiper. The only occurrences of this sandpiper within Katmai National Monument were established by the 1917 expedition of the National Geographic Society. Hine (1919, p. 481) collected one specimen (misnamed red-breasted sandpiper), August 23, 1917, on a sandy beach near the mouth of Katmai River. He noted that the species was not numerous at any time. Presumably another specimen is mentioned by Gabrielson and Lincoln (1959, p. 388) as having been taken at "Katmai" by Clarence F. Maynard, topographer of the expedition, and identified by H. C. Oberholser.

Ereunetes mauri Cabanis, western sandpiper. Large flocks of western sandpipers were common for several days in midsummer of 1917, on sandy beaches in the Katmai-Kashvik Bay area, according to Hine (1919, p. 481). He collected specimens on July 23 and August 2, but observed the species frequently over a longer period. I did not identify it during my stay in the Monument.

Lobipes lobatus (Linnaeus), northern phalarope. A very few individual birds were seen in Kukak and nearby bays during late July and early August, 1953. This scarcity conforms with my observations of 13 years previously when only two records were obtained. One was on Brooks Lake, September 9, and the other at Cape Nukshak, October 7, 1940.

Larus glaucescens Naumann, glaucous-winged gull. This was the most numerous of the gulls and one of the most abundant and widely distributed birds in the Monument. Glaucous-winged gulls were seen every day, both east and west of the Aleutian Range. Although the greatest numbers were along the coast and on the larger lakes and

ivers, the species was often seen on the tundra where numerous ponds provided resting places. It was absent only from the mountains, although even here a transient bird might be seen at intervals.

In general the altitudinal range was sea level to about 1,000 feet. The presence or absence of salmon and of suitable nesting places were the primary factors that influenced the distribution of the birds during the summer season.

Glaucous-winged gulls were recorded in so many localities in the Monument that it would be pointless to list them. The areas of greatest abundance were Mount Pedmar, Kukak Bay, Brooks River and environs, lower Savanoski River, Coville River, and central Naknek Lake. During a violent storm, August 13, 1953, I saw very large numbers of gulls that had taken refuge on Cape Gull, south of Kafliia Bay. Positive identification was impossible from the plane in which I was traveling, but most of the birds probably belonged to this species.

Roughly comparable numbers of gulls seemed to be present in the area during my travels in Katmai National Monument from September 3 to October 7, 1940. In the Shelikof Strait region concentrations of the birds were noted in Kinak Bay and the head of Geographic Harbor. This distribution may be peculiar to autumn; in any event, I did not find especially large numbers in those places during the summers of 1953 and 1954.

During Hine's stay on the shore of Katmai Bay in the summer of 1917, the glaucous-winged gull was also common. It nested all along the sea where suitable rock cliffs were present. He found that the young gulls were fed mainly on the northern razor clam (*Siliqua patula* Dixon). (Hine, 1919, pp. 477-478.)

We found nesting colonies of glaucous-winged gulls in at least nine places. The outstanding site was the steep, sea-facing cliff of Mount Pedmar where several thousands of pairs, presumably mostly glaucous-wings but probably including some short-billed gulls, reared their young in complete safety from four-footed predators. Rock "pillars" near the north shore of Kukak Bay, and a small island about one-half mile west of the pillars, sheltered the second largest group on the coastal edge of the Monument. (Pl. 12, fig. 2.) A somewhat larger colony, probably several hundred birds, used the island in Naknek Lake on the western boundary of the Monument.

Small bands of this gull nested in eastern Brooks Lake (at least 15 nests on 2 islets east and west of the largest island); in Iliuk Arm (about 10 nests on 3 islets east of the Narrows, and "numerous" others on 2 or 3 small islands north of Margot Creek); in eastern Lake

Coville (2 nests on large island) ; and in Grosvenor Lake (about 10 nests on small island one-fourth mile off the central north shore, and about 2 nests at an islet 200 yards south).

The nesting places were varied in plant cover. Some were almost or entirely barren of vegetation, with nothing more than close-clinging lichens. Most of the nests were located in dense grass which furnished some shelter from sun and protection from rapacious fellow gulls. In a few cases gulls built their nests among willow or alder shrubs which occasionally were so dense as to offer resistance to human investigators.

Hatching of the young glaucous-winged gulls extended over a considerable period. In some cases tiny chicks were found after full-grown young were flying and finding their own food. In chronological order, my notes on eggs and development of the young during 1953 and 1954 are as follows: Mostly eggs and several downy young, one of which was old enough to show fear, Brooks Lake, June 29; entire clutches of three eggs in two nests not hatched, Lake Coville, July 16; all eggs hatched except a few probably infertile, and all nests vacated by young, Iliuk Arm, July 16; two nests under incubation, two chicks not yet manifesting fear, and seven immature birds the size of four-month old domestic poultry, Grosvenor Lake, July 24; all young swimming, Iliuk Arm, August 2; several young of the year flying, several large immatures remaining at nests, Kukak Bay, August 6; numerous young swimming and probably capable of flight, and two chicks less than one week old, Naknek Lake, August 17; two juveniles barely able to fly, and a third still downy but growing the wing primaries, Brooks Lake, August 31.

In the past primitive man was enemy No. 1 of this species and other colonial nesting birds. Modern Eskimos in southwestern Alaska now prey less heavily on birds' nests for the eggs, although raids still occur. Because of the distance from established villages, gull colonies in Katmai Monument probably are seldom victimized, although occasional casual raids on a small scale may be perpetrated from fishing boats. Some destruction of gull nests and eggs occurred in the summer of 1953 when topographic survey parties established stations on some of the islands along the coast. I was told of one incident when gull eggs on an island in upper Kukak Bay were smashed inadvertently when the surveyors attempted to run down a "slender, brown animal." From this description and other circumstances, I infer that the creature may have been a mink, which may well have been feeding on the eggs and gull chicks.

In early September, 1953, I watched briefly an adult otter with three young which were moving about on a gull-nesting island in western Iliuk Arm. The mammals became aware of my presence and left before chancing on any of the several young gulls present. It is presumed that otters will feed on these birds when opportunity offers.

Larus argentatus, presumably *smithsonianus* Coues, herring gull. According to my observations this species is usually scarce within Katmai Monument. I noted a very few herring gulls along Brooks River, June 29 and July 9, 1953. About six birds were seen at the mouth of Margot Creek, on the south shore of Iliuk Arm, July 16. I termed the species "numerous" on Lake Coville, September 2, 1953. My remaining records were of a few birds at Brooks River, September 5, 1940, and on Brooks Lake four days later.

Larus canus brachyrhynchus Richardson, short-billed mew gull. (Pl. 12, fig. 2.) This species was common, but much less numerous than the glaucous-winged gull. It was found everywhere in the Monument in the vicinity of water, but seemed more abundant west of the Aleutian Range than along Shelikof Strait. Minor concentrations of short-billed gulls were located in western Lake Coville, at Brooks River, and in Kukak Bay.

A small nesting colony was found in 1953 on a cliff that rose sheer from the water on the north shore of inner Kukak Bay. We saw no other nests of this species anywhere in the Monument, although immature birds were noted quite often in August and early September.

Short-billed and glaucous-winged gulls often associated together in resting, feeding, and other activities. The fact that we found no nests of the short-billed gull in colonies of the more abundant species led us to infer that they are separated during this period. The short-bill seems to nest a month or so later, if activity at the Kukak Bay colony in 1953 was normal and can be used as "standard." On August 6 practically every nest was being brooded but no young were visible. By this date most young glaucous-winged gulls were taking to the water at any disturbance.

Hine (1919, p. 478) recorded numbers of short-bills among the thousands of gulls at Kashvik Bay during the latter half of August, 1917. He took a specimen in immature plumage on August 23. Gabrielson noted the short-billed gull at Brooks Lake, July 10, 1940.

Larus philadelphia (Ord), Bonaparte's gull. Small to moderate numbers of Bonaparte's gulls were distributed over the lower eleva-

tions of Katmai Monument throughout the summer and autumn. The population generally increased markedly by late summer, but the records indicate that this was subject to considerable fluctuation. In 1954 the species was uncommon until mid-August, when I noted that it was the most abundant gull on central Naknek Lake. I also found it rather numerous on the North Arm of Naknek Lake August 25. The preceding year Bonaparte's gull was not recorded until September 2, when I saw large numbers on Coville River and Lake Coville. I also found it on Brooks Lake, September 8 and 9. In 1940 I identified only one Bonaparte's gull in the Monument; it was at the mouth of the Savanoski River, September 20. Hine (1919, p. 478) stated that in 1917 large flocks appeared in Kashvik Bay about the first of August. He collected several specimens on August 2.

Immature Bonaparte's gulls were noticed for the first time in 1954 on July 18, when Schaller saw a number, including several adults, on the mud flats at the mouth of American Creek. Brody recorded 35 adults in winter plumage at the mouth of Brooks River on August 19, 1954, but five days later saw a bird with dark head feathers still unmolted.

Rissa tridactyla pollicaris Ridgway, Pacific black-legged kittiwake. This beautiful species is absent from our area, or very rare, throughout the summer. The earliest seasonal record is that of an immature kittiwake that I saw in a tree south of Research Bay, on the south shore of Iliuk Arm, August 30, 1953. The following year, on August 31, Brody and I observed an immature bird near the eastern end of Brooks Lake. After that date single birds were seen in the same area September 1; on a small lake north of Contact Creek, September 5, 1954; in the North Arm of Naknek Lake September 7; and at Brooks Lake, September 9, 1953. The species was a little more numerous September 4 to 27, 1940, on Iliuk Arm, Brooks River, and Brooks Lake (where I saw about 10 birds in 1 day, September 9).

I found kittiwakes abundant along Shelikof Strait from Katmai Bay to Hallo Bay, October 4 to 7, 1940. Many were seen on the mud flat at the head of Geographic Harbor, and great numbers were feeding on fish (supposedly herrings) that were jumping from the water off Cape Nukshak. I did not find kittiwakes in that region when I was there from July 22 to August 13, 1953, and Hine (1919, p. 477) had a similar experience at Katmai-Kashvik Bays up to about August 10, 1917. Then large flocks of hundreds of birds arrived, and subsequently the kittiwakes at times made up a large percentage of the gulls on Kashvik Bay.

From these data it is inferred that the species is absent from the Katmai area until about mid-August. At that time a few birds appear on the western slope and large numbers flock into the bays on Shelikof Strait. It is not known when they depart or whether some birds winter here.

Two kittiwakes were found dead in the Monument near the end of our 1954 season. Presumably the same bird which Brody and I observed swimming in Brooks Lake August 31, and which seemed quite normal and in immaculate plumage, was found dead by me about 24 hours later. The carcass was limp and apparently death had occurred only a short time before. A hole about $\frac{5}{8}$ inch in diameter penetrated the skin under the left wing but did not extend into the body cavity. The bird appeared undernourished and its stomach was empty except for a little gravel. Schaller made the specimen into a study skin (his field number 156) and furnished the foregoing information as a result of his autopsy.

Less than a week later (September 6), on the shore of a small lake about 3 miles northeast of the junction of Contact and Takayoto Creeks, Schaller found another dead kittiwake. This too was an immature bird with the same type of hole under the left wing. The peritoneal cavity and alimentary canal were crowded with flukes.

Sterna paradisaca Pontoppidan, Arctic tern. This graceful flyer was rather uncommon in Katmai National Monument. It appeared to be confined to the lake country, up to about 200 feet elevation, on the Bering Sea drainage. My seasonal records of the species extend from June 29 (1953) to September 6 (1940).

Arctic terns were noted on Brooks Lake (June 29, 1953, and September 6, 1940), Brooks River (July 31, 1954), Naknek Lake (July 8, 1953, and September 4, 1940), Iliuk Arm ("common," July 16, 1953), mouth of Savanoski River (July 17, 1953, and August 21, 1954), western portion of Grosvenor Lake ("numerous," July 5; "several," July 12; and July 19, 1954); Lake Coville ("common," July 7, 1954); and lower American Creek (July 18, 1954).

A considerable number of terns were seen, July 31, 1954, fishing at the small circular lake about one-quarter mile east of the mouth of Brooks River. The day was windy and Naknek Lake and Iliuk Arm were too rough for the birds, which may have gathered from a wide area to feed on the sheltered pond.

A nesting colony of about 15 pairs of adults was discovered on a bare rock island in Lake Coville about 200 yards from the south shore

and 2 miles west of Coville River. The island was about 30 by 40 feet in area, and at its highest point it extended 5 feet above the current lake level. On the date of our visit, July 9, 1954, two young were downy toddlers while eight others ranged in development from partially fledged birds to weak fliers. One clutch of three eggs was being brooded, and the parents persisted in setting over them while we were taking notes and photographing less than 6 feet away.

Several terns were found on a rocky islet near the north shore of Grosvenor Lake and 3 miles east of Coville River. The birds were so tolerant of our presence that we suspected the spot of being a nesting site. A search revealed one piece of shell of a tern egg, but no other indications of nests or young.

Uria aalge inornata Salomonsen, North Pacific murre. This species appears to migrate into the coastal waters of the Monument only after the nesting and rearing season. No murres were recorded during my summer fieldwork of 1953 and 1954. However, in the fall of 1940 I found the birds numerous from Amalik to Katmai Bays (October 4) and in Kukak and Hallo Bays (October 7). It is possible that some of these birds were Pallas's murres, *U. lomvia arra* (Pallas).

Cephus columba Pallas, pigeon guillemot. Guillemots were rather numerous in upper Kukak Bay during my stay there in midsummer, 1953. I recorded them in my field notes on July 23 and August 3, 6, and 9. It seemed likely that they nested somewhere in the area. A concentration of guillemots near rocky bluffs and cliffs that rose from deep water on the north side of Kukak Bay, 3 or 4 miles northwest of Aguchik Island, was an indicator of the locality.

A few birds were seen in Amalik Bay July 28, 1953. I did not record the species anywhere on Shelikof Strait during the fall of 1940.

Brachyramphus marmoratum (Gmelin), marbled murrelet. The murrelet is scarce on the Katmai coast in summer but I recorded it occasionally early in August, 1953, in Kukak Bay. I saw it commonly from Katmai Bay to Hallo Bay, October 4 to 7, 1940. The birds became more numerous as we proceeded northward, particularly when we reached Kukak and Hallo Bays.

Fratercula corniculata (Naumann), horned puffin. Another post-nesting-season migrant, the horned puffin, has been recorded in the Katmai area only in autumn. I found the species common along the rocky coast from Amalik Bay to Katmai Bay, October 4, 1940.

Lunda cirrhata (Pallas), tufted puffin. A colony of puffins occupied the large cliff on the north shore of the inner entrance to Kukak Bay. The birds, which I estimated at 50 to 100 in number, appeared to be nesting in the steep grassy hillside near the cliff. They were viewed from a boat on several occasions during the last week of July, 1953.

A large assemblage of tufted puffins, together with harlequins and other ducks, was seen in Amalik Bay on the evening of October 3, 1940. This bay and Geographic Harbor, with their rocky cliffs and steep bluffs, appeared to be a good nesting area for puffins. However, I did not have an opportunity to examine it carefully during the two summers of the Katmai Project.

Bubo virginianus (Gmelin), horned owl (race unknown). Horned owls were fairly common in the lowland forests on the Bering Sea slope. We recorded three different groups of young within three weeks in 1954. Two were found by Schaller: A family of three were seen in a cottonwood grove near the north shore of Grosvenor Lake on July 5, and two days later a group of four were flushed from a dead spruce north of Lake Coville. On July 24 Schaller and I saw two more young owls in a cottonwood grove bordering the large stream that flowed into Grosvenor Lake midway of the north shoreline. All these birds were fully fledged and capable fliers.

One horned owl ranged around the outlet of Brooks River throughout the period (July 26-September 2) that we camped there in 1954. We heard it calling often at night and occasionally during the day, and saw it at intervals. Dr. Brody reported it late on the night of August 30 perching atop a high pole in the public camp at the outlet of Brooks River. This owl was a very pale individual, indicating that it was the Saint Michael great horned owl, *B. v. algistus* (Oberholser). I saw two horned owls, June 30, 1953, as they perched near each other in a birch thicket on the bank of Headwaters Creek about a mile west of Brooks Lake.

In three out of five instances, the owls observed by us were associated with cottonwood groves. In all cases the birds were in localities less than 200 feet above sea level.

Surnia ulula caparoch (Müller), American hawk owl. Our only positive identification of this species was made in midmorning of September 11, 1940, when I found two hawk owls in a cottonwood grove at the north base of Mount Katolinat, about 2 miles above the

mouth of the Ukak River. The birds were curious and perched in the half-dead trees within a hundred feet of us for four or five minutes. On two other occasions that year, medium-sized owls that probably belonged to this species were seen in semidarkness. One bird was hunting over the marshes at the outlet of Brooks River on the evening of September 6. The other flew around me late on September 17 when I was on the south shore of Iliuk Arm west of the Ukak River.

Strix nebulosa nebulosa Forster, American great gray owl. The species was observed twice (probably two individuals) on Headwaters Creek within 2 miles of Brooks Lake, during the evening of September 8, 1953. The birds were perched in clumps of spruce about 200 yards apart.

Asio flammeus flammeus (Pontoppidan), northern short-eared owl. The first short-eared owls of record in Katmai National Monument were seen by Schaller. He watched one flying over a marsh near the northeastern shore of Coville Lake, July 7, 1954, and observed the second bird four days later as it sat on a pile of driftwood back of the beach at Hallo Bay. Schaller and I, on July 22, 1954, found a family of two adults and two juveniles perching on a rock bluff that rose from the south shore of Grosvenor Lake about 2 miles east of the portage to the Bay of Islands. One of the young owls seemed to regard us with curiosity as we passed in our boat. It sat quietly, but its companion fluttered wildly to another perch.

Osgood (1904) saw considerable numbers of short-eared owls during his travels west of the present Monument in the fall of 1902. He recorded (p. 69) that the birds were attracted by lights and came to several of his camps on Becharof Lake.

Megaceryle alcyon caurina (Grinnell), western belted kingfisher. A sparse population of kingfishers was widely distributed over the lowland lake country and along the marine boundary of Katmai National Monument. On the coast I saw one bird in the passage between Amalik Bay and Geographic Harbor on October 5, 1940, and another the same day in Kinak Bay.

On the Bering Sea drainage the records are more plentiful. Lone birds were seen by me on Brooks River, September 5 and 9, 1940, late August 1953 (oral report by George Peters), September 7, 1953, and September 2, 1954; on a small tributary stream 2 miles east of the outlet of Savanoski River, August 24, 1953; on Coville River,

September 1, 1953; and at four widely separated points around the shore of Brooks Lake, September 9, 1953. The ecological distribution of the individual birds was as follows: Lake shorelines, four; rivers, four; marine bays, two; and small streams, one.

A kingfisher that was seen on Brooks River several times in the late summer of 1953 visited my camp in a cottonwood grove about one-half mile west of the river's mouth early on September 7. As I cooked breakfast the bird perched overhead in the cottonwoods and rattled persistently and with great vigor for nearly half an hour.

Colaptes auratus borealis Ridgway, boreal yellow-shafted flicker. One individual of this conspicuous species was seen by Gabrielson near the outlet of Brooks Lake on July 10, 1946. It was the westernmost flicker that he has seen in Alaska, and the only one that has been recorded in or near Katmai National Monument. (Gabrielson and Lincoln, 1959, p. 562.)

Dendrocopos pubescens nelsoni (Oberholser), Nelson's downy woodpecker. The sole record of this species in the Monument dates back to September 19, 1940, when I saw a male downy woodpecker in the spruce-cottonwood forest west of the Ukak River between Iliuk Arm and Mount Katolinat.

Picoïdes tridactylus fasciatus Baird, Alaska three-toed woodpecker. This is another very scarce woodpecker within our area, at least during the warmer months. Only two individuals have been identified. The first, a male, was seen at close range, September 12, 1940, at the outlet of the Ukak River. It was foraging on the trunks of spruce that had been smothered by pumice washed down from the Valley of Ten Thousand Smokes.

The second bird, also a male, was observed by Brody and me August 31, 1954, in the spruce forest about one-half mile southeast of the outlet of Brooks Lake. We watched it for several minutes at a distance of only 50 feet. The bird searched busily for food on the trunks of the spruce, usually 2 to 6 feet above ground but at no time higher than 10 feet.

Empidonax trailii trailii (Audubon), alder Traill's flycatcher. This flycatcher was identified on only two occasions, both in 1953. A single bird was seen in birch-willow scrub near the ruins of the church at Kaguyak Village site, July 29. Another individual was found in cot-

tonwood forest 2 miles southeast of the outlet of the Savanoski River on August 19. The former locality is on Shelikof Strait, a few feet above sea level; the latter is near the western foothills of the Aleutian Range and about 100 feet in altitude.

Nuttallornis borealis (Swainson), olive-sided flycatcher. Two olive-sided flycatchers were seen near each other in a spruce-willow-birch thicket near the southeastern shore of Brooks Lake on September 9, 1953. The birds sat quietly and allowed me to watch them for at least 5 minutes from a distance of less than 50 feet.

Tachycineta thalassina lepida Mearns, northern violet-green swallow. This beautiful swallow was numerous at two localities in the lake country west of the mountains. It seemed to be restricted to these two areas, each of them about 2 miles in diameter, and I never saw it elsewhere.

The largest concentration of birds was noted July 5, 1954, around a prominent rock cliff that formed part of the north shore of Grosvenor Lake, about 2 miles east of Coville River. Presumably they were nesting here in small crevices, as were a pair of rough-legged hawks on a high ledge. These swallows hunted insects in the surrounding region, and many of them were seen July 12 and 24, 1954, as they darted over a marsh and cottonwood forest a mile or two east of their cliff. They were flying in approximately equal numbers with tree swallows.

A relatively small number of violet-green swallows—an estimated 20 to 30 birds—were seen July 15, 1953, and July 31, 1954, flying about over the circular lake east of the outlet of Brooks River. On the former date two swallows came into our camp in a little cove of Naknek Lake 1 mile north of the river. They darted and hovered for almost half an hour, feeding on flies that multiplied in a refuse pile near our pathologist's worktable. They showed no fear of us as we sat working and writing notes within 20 feet of their food source.

Iridoprocne bicolor (Vieillot), tree swallow. I made positive identification of this species at only one locality in Katmai Monument. This was near the north shore of Grosvenor Lake about 4 miles due east of Coville River. Many tree swallows, in company with approximately equal numbers of violet-green swallows, were seen feeding on July 12 and 24, 1954. The area was partially open marsh, backed by a large expanse of cottonwood forest. A stream about a foot deep and 15 to 20 feet wide ran swiftly through it to empty into Grosvenor Lake.

One tree swallow was tentatively identified over lower Brooks River on July 26, 1954, and several juveniles at a nearby lake on July 31. In each case the birds were darting among numerous bank swallows and it was impossible to get a clear view of them. However, Gabrielson recorded seeing "a few" tree swallows, July 20, 1940, over the northeastern shore of Brooks Lake. This was only a mile, or less, from the area on lower Brooks River. (Gabrielson, 1944, p. 276.)

A presumed nest was found July 12, 1954, in mixed spruce-cottonwoods on the beach dune near the north shore of Grosvenor Lake. (See first paragraph, above.) As I stood looking at a 1-inch round hole about 10 feet above the ground in a decrepit and broken-topped cottonwood, three adult tree swallows gathered to perch on twigs within 5 feet of my face. They sat there in silence, watching me in apparent anxiety, until I left the scene without risking destruction of the tree (and nest) by trying to climb it.

Riparia riparia maximilliani (Stejneger), American bank swallow. Bank swallows were concentrated in two areas within the Monument. One of these was Swikshak Lagoon, where, on August 4, 1953, I saw great numbers of the birds feeding on insects that swarmed over the brackish marsh. The other area was centered on lower Brooks River, where I first recorded the species on July 9, 1953. Numerous tunnels were in the sheer eroded bank on the east side of the river about 300 yards below the falls, and the swallows were often seen entering them during late July and the first half of August, 1954. One of the favorite feeding places of this colony was over a circular pond about one-quarter mile east of the mouth of Brooks River. Here, on July 31, 1954, I saw large numbers of the birds catching insects, in company with a few violet-green swallows and (probably) tree swallows.

Gabrielson (1944, p. 277) recorded the species as "fairly common" near the outlet of Brooks Lake, July 21, 1940.

Perisoreus canadensis arcus Miller, Alaska gray jay. While they could not be termed "abundant," gray jays were widespread and came often to the attention of the bird watchers. We were never long in camp or on the trail in wooded or partially wooded areas of the Monument west of the Aleutian Range before being greeted, usually with complaining calls, by this species.

As in the case of other very common birds, I did not record every instance of encounters with the gray jay. However, the list from my field notes is as follows: Brooks River and vicinity, early September,

1940, August 15, 1953, July 31, August 14, 19, and 31, and September 1, 1954; Brooks Lake, September 9, 1940; Headwaters Creek, September 8, 1953; lower Savanoski River, September 13 and 23 ("common"), 1940, July 17, August 19 and 20, 1953; 2 miles north of outlet of Savanoski River, August 16, 1953; lower Ukak River, September 10, 11, and 18, 1940 ("common"), and August 2, 1954; middle reaches of Ukak River, September 14, 1940; north slope of Mount Katolinat, September 20, 1940 ("common"); portage trail, the Bay of Islands to Grosvenor Lake, September 1, 1953; north shore of Grosvenor Lake, July 5, 1954; Coville River, July 5, 1954.

Rather oddly, I did not find the jay in the coastal fringe along Shelikof Strait. A weak flier, it probably would not be able to cross the Aleutian Range directly, but there was no evident obstacle against gradual infiltration around either the northern end of the mountain chain or through the passes near Becharof Lake. The species, however, is distinctly a lowland dweller. I never found it at elevations more than 500 feet above sea level.

In its ecological requirements the gray jay is not demanding, provided some scattered trees, or at least thickets, are available. My occurrence records for 1953 and 1954 show that I found it in spruce forest and in willow thickets interspersed with grassland on four occasions each; in cottonwood groves and alder-covered stream or lake margins, three times each; and in spruce-alder and mixed woods, twice each.

The species is mildly gregarious and I found lone individuals only once or twice in the Katmai area. Usually the birds were in twos, threes, or fours. The largest group noted contained "six or eight" members and stayed around a camp of fishery investigators at the outlet of Brooks Lake early in September, 1940. The flock may have been built up by the availability of table scraps and kitchen leavings.

Brody noted that the plumage of this species apparently varied somewhat in color. Some individuals were quite dark, while others were almost pearly gray.

Pica pica hudsonia (Sabine), American magpie. The observer who works for several months in the Katmai area is tempted to rate the magpie as "abundant." Actually, it occurs sparingly to commonly, but the bold, inquisitive nature of the species brings it to notice on many occasions when more populous kinds would be overlooked.

The magpie was almost universal in its distribution within the Monument. It was found in all types of woodland, in mixed thickets

and grassland, and on lake shores and river banks (where it fed, often with gulls, eagles, and brown bears, on dead and decaying salmon). My notes indicate that I saw the magpie most frequently in cottonwood groves, willow thickets interspersed with grassland, and on shores of lakes and streams. However, I also met with it in mixed woodland, spruce forests, and alder-cottonwood stands.

This handsome bird was recorded in so many localities that to list them would be superfluous. The catalog would include practically all named features and locations that I visited along the coast of Shelikof Strait and in the extensive western lowlands. The highest elevation where the magpie was encountered was 800 feet, on lower Windy Creek. The largest numbers were seen in the vicinity of Brooks River, where artificial food in the form of garbage at camps was responsible for the concentration. On one occasion, July 31, 1954, I counted 17 magpies in one group near the east bank of lower Brooks River, and undoubtedly overlooked several birds as they shifted about. At one time, 14 magpies were perched in one small tree. Most of the group were juveniles, and all the birds were squawking and chattering almost continuously.

It is presumed that the species is a year-round resident of the Monument, but seasonal fluctuation in numbers, if any, is unknown. We recorded magpies from the earliest opening of our fieldwork, near the end of June, to the latest observations in October. An apparent peak of abundance occurred in July when the juveniles were in their greatest numbers. Very curious, noisy and unwary, they impressed the observer with their abundance.

Young magpies were flying in the Katmai area by the first of July, if not earlier. In 1954 Schaller and I came across three family groups, each containing four juveniles. Two were seen at different points around Lake Coville on July 7 and 9; the third was noted July 12 on the north shore of Grosvenor Lake about 3 miles east of Coville River. Where food was abundant, as it was near Brooks River, several families might join together for a time in a loose assemblage. This concentration of birds, which was so evident in late July and early August, 1954, had largely dispersed by mid-August.

We were entertained at times, and occasionally annoyed, by some half-dozen magpies that visited our camp west of Brooks River during August, 1954. The birds came, often several times daily, to pick over the nearby garbage pit and to examine the camp for anything interesting to a magpie. If left lying out-of-doors, almost any small objects, especially bright things such as scissors, were likely to be taken. On

one occasion, I watched a magpie pick up a piece of soap on our outdoor table, fly to the ground nearby, and cover it carefully with fallen leaves. The bird then flew to a neighboring tree, but another magpie, which had observed the caching, descended to the spot and uncovered the soap. The second bird was about to abscond with it when the first magpie flew back with great sound and fury to recover its prize from the interloper. The original finder of the soap flew off with it, chattering indignantly, and disappeared in the woods.

Corvus corax principalis Ridgway, northern common raven. This species was seen less frequently in 1954 than during the preceding season or in September-October, 1940. At best, ravens were not numerous in the Monument. They were distributed widely, however, and being conspicuous and vocal they came to notice quite frequently. I found no marked differences in the population density between the Pacific and Bering Sea slopes of the area.

In the Katmai region the raven was found from sea level to nearly 2,500 feet elevation. It was recorded 6 times above 1,000 feet as compared with 23 times below that level. This relative weight of 4 to 1 may not be an accurate comparison of the preference of the species for lower country, because several factors conspired to favor low-altitude observation. On the whole, however, ravens spent much time in summer along the lakes and rivers where salmon was a readily available food. In 19 cases when the species was seen resting or active in an ecological environment (as opposed to flying from place to place), it was on lake or stream margins 8 times, in tundra 5 times, in mixed forest 4 times, and in spruce forest twice. Mount Dumlupınar-Brooks River and Mounts LaGorce and Katolinat were especially favorable areas in which to see ravens.

This species is a year-long resident of the region, and we saw it at intervals throughout the entire period of fieldwork. During the 1953 season I recorded ravens 9 times in July and only 3 times throughout August. The largest group contained 10 individuals. These birds were resting on the gravel beside the outlet of the large stream which emptied into the north side of the head of Kukak Bay. At times around the first of August, 1954, the cacophony along Brooks River below the falls indicated that similar if not larger numbers of ravens were gathered there. However, a majority of this discord was contributed by a brood of five juvenile ravens that stayed in the vicinity until late in the month.

The raven is one of the bird species that may be seen occasionally

in or over the barren area of the Valley of Ten Thousand Smokes. Dr. Curtis told me that about August 15, 1954, he heard ravens, probably two in number, calling from far over camp near the head of Knife Creek. Coming out of the tent, he was unable to see them and concluded they were at a very high altitude.

Nucifraga columbiana (Wilson), Clark's nutcracker. It was not until I had devoted a total of three months to field observations in Katmai National Monument that I saw my first Clark's nutcracker in the area. This occurred August 16, 1953. As I stood on the crest of a rocky knoll in the flat marshy country east of Mount LaGorce and 2 miles south of Grosvenor Lake, the bird alighted in a low tree about 50 feet away. After calling at me for several minutes, it abruptly launched itself into the air, dove steeply into the cottonwoods nearly a hundred feet below, and vanished. I never saw another nutcracker during the entire time that I spent in the region.

Parus atricapillus turneri Ridgway, Yukon chickadee. The two species of chickadees were widely distributed on the Bering Sea drainage of the Monument below 800 feet elevation. Strangely, I never saw any individuals of either species along the coast of Shelikof Strait. Osgood (1904, p. 80) collected specimens of *P. atricapillus* at Puale Bay in October, 1902, and Hine (1919, p. 486) took specimens of the same species from flocks that appeared around his expedition camp on Katmai Bay just before the middle of July, 1917. The latter area is near the southern end of the coast within the Monument, while Puale Bay is about 15 miles outside. Possibly chickadees have failed to work their way northward along the coast across the barriers of high ridges, glaciers, open bays, and wind-swept headlands.

The two species of chickadees can be distinguished readily in the field by appearance and voice. The Yukon chickadee is a little larger, its darker plumage is distinctly black, and the call is clear and high-pitched. The boreal chickadee is smaller, the black cap and throat are suffused with rusty, and its voice is hoarse and lower in pitch.

Both species inhabit a wide variety of woodland and shrubby areas, closed and open. My field notes show that the Yukon chickadee was recorded in the following vegetation types: Cottonwood-willow-spruce (six occasions); cottonwood grove (five times); birch-willow-spruce (four times); spruce, birch-willow, alders, and willow thickets (three times each); birch-willow-cottonwoods, spruce-alder-willow, and birch thickets (twice each). The species appeared to be most

abundant in cottonwood groves, pure spruce forest, and mixed coniferous-deciduous woods. The distribution did not appear to be affected by the presence or absence of streams or ponds. Chickadees were so universal that a list of localities where they were recorded in the Monument would be tedious and without much value. However, the spruce and mixed deciduous woodland on each side of Brooks River was particularly good chickadee territory. Here, as well as elsewhere, it was easy to attract from five to a dozen birds by "squeaking."

Parus hudsonicus columbianus Rhoads, Columbian boreal chickadee. Specimens of the boreal chickadee collected by Gabrielson at Brooks Lake, July 19, 1940, proved to be somewhat intermediate in their morphological characters between the above race and *P. h. hudsonicus*. The racial designation used here agrees best with the geographic distribution of both forms in southwestern Alaska. (Gabrielson and Lincoln, 1959, p. 630.)

The boreal chickadee is easily distinguished in the field from the preceding species. (See second paragraph of the preceding account.) The "brown-cap" or boreal chickadee was the more abundant, at least in the Brooks River and Savanoski areas. On several days in mid-August, 1954, I estimated that in the spruce woods east of Brooks River the "brown-caps" outnumbered the Yukon chickadee two or three to one.

Both species occupied the same habitats (see preceding account) although the boreal chickadee seemed to favor spruce forests more than deciduous woods and thickets. Mixed groups were seen on a few occasions, but as a rule the two species appeared not to mingle. The exceptions may have resulted from a mutual curiosity or excitement regarding the human intruder in the wilderness. The boreal chickadee was the more excitable and the bolder of the two species, often approaching me within a few feet.

Like the Yukon species, I found the boreal chickadee only on the Bering Sea slope of the Monument. It seemed to range at lower elevations only, within 400 feet of sea level.

Certhia familiaris montana Ridgway, Rocky Mountain brown creeper. The brown creeper was added to the Katmai bird list August 18, 1954, when Brody observed an individual in a spruce on the east side of Brooks River. A week later Ward reported seeing a creeper, probably the same one, in the area.

This sight record is listed under the race *montana* on the basis of

specimens that have been collected in the Anchorage region and on Kodiak Island. Several other field observations also are on record from the Kenai Peninsula and the Kodiak Island group.

Cinclus mexicanus unicolor Bonaparte, northern dipper. The species is included among the birds of the Monument on the basis of a single record. I saw one dipper at the falls on Brooks River, September 5, 1940. Three persons in our party, in addition to myself, watched the bird for 10 minutes, from a distance of less than 50 feet, as it searched for insects on the very brink of the waterfall. A careful watch on this section of the river in 1953 and 1954 did not disclose any sign of this interesting species.

One specimen of the northern dipper was taken October 18, 1902, by Osgood (1904, p. 80) on a small mountain stream at Puale Bay, a short distance outside of the Monument on Shelikof Strait.

Turdus migratorius migratorius Linnaeus, eastern robin. In my experience the eastern robin is an extreme lowland bird in this region and rather seldom gets into the western portion of Katmai Monument. The species is numerous—even abundant—in the vicinity of Naknek and King Salmon during the summer and early fall. I saw many robins at King Salmon late in June, 1954, and at Naknek and along the Naknek River up to Big Creek, September 3-4, 1940. However, I found the species in comparable numbers only once close to the Monument. This was among stunted spruces and willows of the tundra along Headwaters Creek, within a mile or two of the west boundary, on June 30, 1953.

On the other hand, Gabrielson saw "many" eastern robins near Brooks Lake, including spotted young, on July 20, 1940. (Gabrielson and Lincoln, 1959, p. 650.) He noted that the species was present in the same locality July 9 and 10, 1946. He considers that the bird is "found commonly . . . in the timbered sections of the Alaska Peninsula." (Ibid., p. 651.)

Schaller saw a lone robin perched on the limb of a dead alder near the tundra at Idavain Lake August 29, 1954. The elevation here was about 600 feet—the highest that the species has been known to go within the Monument.

Ixoreus naevius meruloides (Swainson), northern varied thrush. This species is scarce in the Monument, and its distribution, based on the six records available, is limited to the lowlands west of the Aleutian

Range. It has a narrow altitudinal range—50 to 600 feet above sea level.

The earliest seasonal observation was made July 5; the latest, August 29. Birds were seen in cottonwood forest with alder-spruce understory near Savanoski, August 20 and 27, 1953; among alders on the northwest shore of Grosvenor Lake, July 5, 1954; in willow shrubs near Coville River, July 7, 1954 (by Schaller); in willow-birch thickets near the falls of Brooks River, August 1, 1954; among spruce with willow-birch shrubs on the west boundary of the Monument, August 17, 1954 (by Brody); and in an alder thicket at Idavain Lake, August 29, 1954 (by Schaller). Single birds only were seen in all except the first instance, when two birds were observed.

Hylocichla guttata guttata (Pallas), Alaska hermit thrush. This species was the most abundant thrush and was common in many places in the western lowlands of the Monument during the 1954 field season. I recorded it as early as July 5 of that year and for the last time on September 1, with 10 additional observations between those dates. However, I saw the hermit thrush only twice in 1953, on August 16 and 20. It was not found at all in 1940, but since I reached the Monument so late in the year (September 5), the southward movement may have been well advanced. Earlier that year, on July 19, Gabrielson saw several hermit thrushes near the outlet of Brooks Lake. He also found the species in the same area, July 9 and 10, 1946. (Gabrielson and Lincoln, 1959, p. 658.)

The localities where the hermit thrush was recorded during the period of the Katmai Project included Savanoski, north base of Mount Katolinat, Brooks River region, north base of Mount LaGorce, and various points near the shore of Coville and Grosvenor Lakes. The elevation of all these places was between 50 and 300 feet.

I did not see the hermit thrush anywhere on the coastal area along Shelikof Strait. Hine (1919, p. 486) recorded it in the Katmai River valley and took a specimen, July 25, 1917, but he considered the species uncommon.

Ecologically, the hermit thrush lives in woodland and shrubby areas. In 12 instances when I kept notes on the environment, the species was seen three times in alder thickets with admixture of willow-cottonwood-spruce; twice each in cottonwood forest, willow-birch, willow-grassland, or spruce forest; and once in pure alder thicket.

Schaller found three nests of hermit thrushes in 1954. The first was 3 feet above the gravel beach of northeastern Lake Coville in a de-

pression of a mossy bank that was overhung by a few alders. When discovered on July 7 the nest contained four eggs, three of which hatched about July 18. The fourth egg was fertile but was lying outside of the nest when it was checked on July 19. The second nest, which was found within an hour or so of the first, also had four eggs. It was built about a foot above ground in a willow bush. The third nest, from which the bird was flushed, was found July 15 within 200 feet of nest No. 1. The last discovery also held four eggs and was on the ground beneath a birch.

Hylocichla minima minima (Lafresnaye), northern gray-checked thrush. A specimen of this species was collected by Gabrielson July 10, 1946, near the outlet of Brooks Lake. (Gabrielson and Lincoln, 1959, p. 664.) Schaller watched one of these thrushes for about 10 minutes as it flitted around him in a brushy area near Lake Coville on July 5, 1954, and I saw another bird in spruce-birch-willow growth near the south shore of Lake Coville on July 9 of the same year. Schaller heard the gray-checked thrush sing on quiet evenings around our camp on Coville River during the period July 5-20. The species is shy and may have been somewhat more abundant in lower, thicket-covered localities than is indicated by these few records.

Phylloscopus borealis kennicotti (Baird), Kennicott's Arctic willow warbler. A group of three birds of this species was observed by Gabrielson July 19, 1940, at the edge of the spruce on the shore of Brooks Lake near its outlet. He collected one bird, a newly fledged male, near a small, dense willow. These warblers reminded him of the Tennessee warbler, although they were more nervous and excitable than that species. (Gabrielson, 1944, p. 280.)

Regulus satrapa olivaceus Baird, western golden-crowned kinglet. I found golden-crowned kinglets rather numerous in the spruce grove where we camped July 5-14, 1953, in a cove on the south shore of Naknek Lake about 1 mile north of Brooks River. A few birds were seen July 17, 1953, in mixed willow-birch-alder-cottonwood growth near Savanoski. The species appeared to be quite localized in distribution within the Monument.

Regulus calendula cineraceus Grinnell, western ruby-crowned kinglet. Gabrielson saw a male and a female of this species near the outlet of Brooks Lake on July 10, 1946. He also heard another male

singing nearby. (Gabrielson and Lincoln, 1959, p. 686.) Apparently these are the only members of their species that have been recorded in the Monument or vicinity.

Anthus spinoletta pacificus Todd, western water pipit. The pipit is typically a bird of the open tundra, from 1,000 feet elevation upward. All the large flocks of pipits seen in the Monument have been in that type of habitat.

My first recording of the species was on July 11, 1953, when Schiller set traps for mice and other small mammals near the crest of Mount Dumlup. Six pipits were caught in about two days' time. This, incidentally, was greater than the number of mice and shrews captured in the same trap lines. Pipits were fairly numerous on the mountain above the 1,200-foot contour (approximately). George Schaller found the species "numerous" when he climbed to the same mountaintop on August 1 of the following year.

I saw a few pipits August 17, 1953, in the grassland with occasional alder clumps at an elevation of 1,000 feet 5 miles north of Yori Pass. Larger numbers were seen later the same day on typical tundra at about 1,500 feet elevation between the Bay of Islands and Idavain Lake.

The most spectacular show of this species was enjoyed August 29, 1954. On the tundra north of Idavain Lake, between 1,200 and 2,000 feet above sea level, we saw many flocks ranging in size from a dozen to several hundred birds. In the aggregate the number must have totaled many thousands of individuals. In the larger flocks, pipits were associated with Alaska Lapland longspurs in the proportion, which I estimated, of 60 pipits to 40 longspurs. The sight of the larger flocks of birds wheeling and gyrating in the sunlight across the desolate rolling mountains was spectacular. One large band of the birds pursued and swarmed around a male goshawk after he (perhaps playfully) swooped into and through the assemblage without making a catch (see p. 101).

In small numbers pipits move into the low country during August. We watched three birds walking about after insects among clumps of grass on the pumice beach west of the outlet of Margot Creek, on the south shore of Iliuk Arm, August 21, 1954. Two days later a lone individual searched for insects along the south shore of Naknek Lake west of Brooks River. A migration of pipits was noticed by Hine in 1917. He saw no birds until about the first of August, after which they were common on the beaches of Katmai and Kashvik Bays. Hine (1919, p. 486) took specimens on August 10.

An interesting observation was made by Schaller when he found a lone pipit sitting on a chunk of lava in the desolation of upper Knife Creek, at 2,000 feet elevation, on August 5, 1954.

Lanius excubitor invictus Grinnell, northwestern great shrike. The species was comparatively common west of the Aleutian Range when I was in that area during the period September 5-27, 1940. A single bird and a pair were seen at Brooks River, "several" on the lower northern slope of Mount Katolinat, and one individual on lower Windy Creek. Shrikes were numerous along the lower course of the Ukak River.

It is probable that shrikes were migrating through the region during this three-week autumn period in 1940 and were more plentiful than normally. In any event the number materially exceeded the tally of birds recorded during nearly five months of fieldwork from late June to early and mid-September, 1953 and 1954. The only two birds seen in 1953 constituted fall records—September 6 and 8, near Brooks River and on Headwaters Creek, respectively. In 1954 a family group of an adult and four juveniles was found July 9 near the south shore of Lake Coville. Schaller watched a shrike on July 11 as it attempted to catch a small bird on the grassy plain at Hallo Bay. (See detailed account below.) Later, from August 21 to 24, one shrike was observed several times at the outlet of Brooks River.

The family of shrikes seen July 9 near Lake Coville probably was in its home territory (as compared with the other birds, which presumably were migrants). The vegetation there was young willow and birch 6 to 9 feet high, and clumps of larger alder and spruce. The juvenile birds were capable fliers and were extremely noisy. I watched one of them for some time as it perched in an isolated dead spruce and tore at an object that appeared to be a dead mouse.

The shrike that was recorded on Headwaters Creek, September 8, 1953, was engaged in hazing an osprey. The latter sat in the top of a spruce and "killy-ed" as the shrike made repeated passes, chattering as it did so.

Schaller observed an encounter between a shrike and a small bird. His account (from MS. report) is as follows: "At Hallo Bay in the Shelikof Strait area, on July 11, 1954, I watched an interesting attempt by a shrike to catch what I believed to have been a Savannah sparrow. At first the shrike sat motionless on top of a dead spruce. Suddenly it folded its wings and dived into the brush below. A startled sparrow shot into the air, and strove to escape by reaching the safety

of the brush again. But the shrike pushed and harassed the sparrow from below till both birds were about thirty feet above ground. Without warning, the shrike suddenly climbed above the sparrow and endeavored to grab it. With a sideways twist the sparrow eluded the shrike, but still could not reach the shelter of the brush. This aerial maneuver was repeated several times till the sparrow finally escaped. The shrike returned to its perch—probably quite frustrated."

Vermivora celata celata (Say), eastern orange-crowned warbler. I saw orange-crowned warblers on four occasions, all in July 1954. A lone bird was observed July 8 in a birch–willow thicket near the north shore of Lake Coville, and several more were seen the same day in spruce–birch–willow woods at another locality on the same shoreline. A small number of birds were found July 9 in birch–spruce thickets on an island near the south side of Lake Coville. The species was also identified July 22 in a cottonwood grove on the south shore of Grosvenor Lake 6 miles northeast of Hardscrabble Creek.

Other individuals of the same species were noted in 1954 by Schaller, who saw two birds in thick willow brush on the east shore of Lake Coville during mid-July; and by Brody, who found one bird in willow growth along the west shore of lower Brooks River on August 31. Gabrielson recorded the species near the outlet of Brooks Lake, July 10, 1946. (Gabrielson and Lincoln, 1959, p. 712.)

This brief list of observations indicates that in the Katmai region the orange-crowned warbler is a rather uncommon summer resident in mixed deciduous thickets and woods at elevations within 300 feet of sea level.

Dendroica petechia rubiginosa (Pallas), Alaska yellow warbler. Hine (1919, p. 486) saw this species often in wooded areas near his Katmai Bay camp in the summer of 1917. Although he never found a nest, he felt certain the species was breeding there. Farther north, in a patch of spruce on the great flat at Hallo Bay, my assistant, George Schaller, noted two individuals during the hour or two that we tramped the area on July 11, 1954.

West of the Aleutian Range the yellow warbler was rare during the breeding season. The sole record was made by Schaller of a single bird at Grosvenor Lake, July 22, 1954. The species was more numerous later that season and we saw a few adults in fall plumage during the last two weeks of August. These birds were among spruces near the outlet of Brooks Lake and in cottonwood–willow thickets west

of lower Brooks River. Brody noted that the species often foraged with the northern pileolated warbler. All these localities are less than 200 feet in elevation.

Hine collected a specimen of the yellow warbler July 12, 1917, at Katmai Bay.

Dendroica coronata hooveri McGregor, Alaska myrtle warbler. Seasonal records of the myrtle warbler in the Monument range from July 10 (1946) to August 20 (1953 and 1954). Although scarce during July, it became numerous or even abundant during the migration of mid-August. The species seemed to be limited to altitudes below 600 feet west of the Aleutian Range. We did not record it in the lowlands along Shelikof Strait.

I found myrtle warblers, often with pileolated or sometimes yellow warblers, in brushy areas and in the lower story of the forest. They showed no marked preference for any one vegetation type. My field notes reveal that the species was seen five times in spruce forest, with or without various admixtures of birch, willow, or alder; twice in cottonwoods or cottonwood-willow-spruce; and twice in willow with alder, birch, or cottonwood. I rated it as "abundant" once, in the spruce forest east of Brooks River on August 14, 1954. About half (five out of nine) of my records of the species came from the Brooks River region, where Gabrielson also saw it July 10, 1946. The other localities where I noted it were Savanoski, Hardscrabble Creek north of Rainbow River, and the south shore of Lake Coville. Schaller saw this warbler near Iliuk Arm and the North Arm of Naknek Lake.

I found a juvenile bird, or an adult in fall plumage, on July 26, 1954, near Brooks River. Brody noted that all birds of this species seen by him after August 16 were in their fall dress.

Dendroica striata (Forster), blackpoll warbler. This handsome warbler is scarce or local in distribution within Katmai Monument. It was never recorded until July 5, 1954, when Schaller heard two birds calling in a cottonwood grove west of Grosvenor Lake. He later saw one of them. Four days later I saw several blackpolls in a mixed stand of spruce, birch, and willow near the south shore of Lake Coville. On July 11, Schaller noted a single individual at Hallo Bay.

One member of the loose flock of birds seen near Lake Coville on July 9, 1954, was collected by Schaller in a willow creek bottom. It was a male, already in fall plumage, with testes measuring 2×1 , 2×1 mm. He assigned to the skin his field collecting number 149.

Seiurus noveboracensis notabilis Ridgway, Grinnell's northern water thrush. On five occasions lone individuals of this species were seen by me along or within a quarter of a mile of Brooks River. In at least four cases these were different birds. They were recorded twice July 31, twice August 1, and once August 19, 1954.

Schaller saw two water thrushes July 18, 1954, in a willow-alder thicket on lower American Creek. He succeeded in collecting one of these as a specimen (his number 153). It proved to be a female with very small ova.

All the approximately half-dozen birds seen by us were at elevations of about 100 feet. One was among a few alders near the edge of a spruce forest, the others in dense thickets—two in willow-alder and the remainder in pure willow growth.

Wilsonia pusilla pileolata (Pallas), northern pileolated warbler. This was by far the most abundant warbler in the Monument. It was conspicuous in a number of localities around Lake Coville, Grosvenor Lake, North Arm of Naknek Lake, Brooks River, Savanoski, and Hardscrabble Creek, at elevations ranging to 600 feet above sea level. Hine (1919, p. 486) stated that the pileolated was the most plentiful warbler in lower Katmai River valley during the summer of 1917. However, I did not find the species at all in the course of my work along Shelikof Strait during 1953 from July 23 to August 14, and saw only a few individuals on July 11, 1954, at low elevations in Kuliak and Hallo Bays. During the period of the Katmai Project the pileolated warbler appeared to be much more numerous west of the Aleutian Range.

Pileolated warblers had arrived and were nesting before my arrival in the Monument at the end of June in both 1953 and 1954. My final seasonal record of the species in 1953 was August 27, but the next year I did not see it after August 20. (However, Brody noted one male, just beginning to change to fall plumage, on August 30.) I did not find it at all in 1940, in which year I reached the area September 4. The evidence is good, therefore, that the migration was virtually completed by the end of August.

My notes show that the species was especially abundant August 19-20, 1953 (at Savanoski and on Hardscrabble Creek), and August 1 and 14, 1954 (Brooks River area). Excepting the August 1 date, therefore, the migrating birds became unusually numerous in each case about a week before the last individual was observed. At such times the woods and thickets were almost "alive" with birds. On one

occasion (August 19, 1953) a few "squeaks" attracted at least 15 and perhaps as many as 20 pileolated warblers. Another time (August 1, 1954) about a dozen came to investigate.

The habitat of this species comprises thickets and the understory of all types of woodland. During the two summers at Katmai I recorded it in cottonwood groves (including admixtures of spruce, alder, or willow), nine times; in willow thickets, eight times; in spruce forest (usually with more or less alder understory), seven times; and in birch or birch-willow thickets, three times. In these environments it was usual for the Wilson's warbler to forage in company with other warblers—myrtle, yellow, and orange-crowned.

Euphagus carolinus (Müller), rusty blackbird. This species was found in moderate numbers at ponds and marshes and along a few streams in the western lowlands of the Monument. It was very much localized, being recorded at only six areas, all less than 200 feet above sea level. They were as follows: Pond east of the outlet of Brooks River; small tributary of Savanoski River a mile or two east of Iliuk Arm; Savanoski; pond south of Grosvenor Lake (observation by Schaller); north shore of Grosvenor Lake 4 miles east of Coville River; and marsh at the west end of Lake Coville. Environmental preference was shown by the record of occurrences; the species was found three times around ponds, and once each at a marsh, a marshy lagoon, at beaver ponds on a small stream, in a cottonwood grove bordering a rocky stream, and on a spruce-covered ridge near a marshy stream.

Rusty blackbirds apparently migrated from the Katmai region in late summer. The earliest observation was made June 30 (1954); the latest was August 20 (1953).

Molothrus ater (Boddaert), brown-headed cowbird (race unknown). On September 2, 1953, I saw a male cowbird in an alder clump near the southwest shore of Lake Coville. The bird stayed in view about 75 feet away for a minute or two, then disappeared into dense thickets. This is the only record of the species in the Katmai region.

Pinicola enucleator flammula Homeyer, Kodiak pine grosbeak. This distinctive species is included in the list on the basis of an observation by William F. Thompson, Jr., geographer of the Katmai Project. On July 26, 1953, he told me that about four days previously he had seen

a male pine grosbeak in a willow thicket at an elevation of 1,000 feet on the ridge southwest of Kukak Bay. Mr. Thompson was well acquainted with the species as a result of previous field experience in southwestern Alaska, and there is little doubt of the correctness of his identification.

Leucosticte tephrocotis (probably *littoralis* Baird), Hepburn's gray-crowned rosy finch. Several finches were seen flying and walking over the tundra on the crest of Mount Dumpling early in July, 1953. One bird, a female or juvenile, was killed in one of a number of snap traps that were set by Schiller for small mammals near a streamlet that ran through a moist swale. Unfortunately, the skin was not saved. The birds probably belonged to the race *L. t. littoralis*. Other birds inadvertently captured in the same habitat were western water pipit (six), Savannah sparrow (two), and golden-crowned sparrow (one).

Acanthis hornemanni exilipes (Coues), Coues' hoary redpoll. On the dunes near the beach at Katmai Bay, north of the mouth of Katmai River, I saw a group of hoary redpolls, October 4, 1940.

Osgood (1904, p. 72) stated that the species was common around Becharof Lake and at Puale Bay, October 1-26, 1902. He took specimens in both areas, which are only a few miles outside of, and similar ecologically to, portions of the southwestern region of Katmai National Monument.

Acanthis flammea flammea (Linnaeus), common redpoll. This species occurs erratically in the Katmai area. We obtained several records, all in 1954. Schaller saw three common redpolls in some spruces near Lake Coville on July 7 and a flock of about 50 on Mount Dumpling, August 1. The latter flew from the direction of the high tundra, passed the observer who was at an elevation of about 1,300 feet, and continued down toward the lowlands. Jointly, on July 1 we observed a group of some 20 birds that were feeding in an isolated patch of spruce on the tip of the promontory that divided the head of Kuliak Bay into two coves.

A few lone birds were seen daily near Brooks River from about August 10 until the 30th, 1954. Then a major "wave" swept through the area. For several hours in the morning redpolls were numerous in the cottonwoods around our camp. Brody reported seeing flocks of 30 or more birds moving through the spruce forest east of the river. He watched one group of 30 feeding on willow seeds in the willow

thickets west of the stream between the falls and Naknek Lake. These birds were mostly juveniles—only one truly red “poll” was seen. Brody estimated his day’s total count at 150 birds.

Hine found that common redpolls appeared at Katmai Bay about the middle of July, 1917, and were soon numerous everywhere in the Katmai River valley and on the surrounding mountains. On one occasion a large flock was seen flying about over the Valley of Ten Thousand Smokes. Hine (1919, p. 483) collected specimens on July 23, 1917. Ridgway, as a member of the Harriman Alaska Expedition of 1899, collected 10 birds at Kukak Bay. These specimens are in the United States National Museum. (Gabrielson and Lincoln, 1959, p. 761.)

Loxia leucoptera (probably *leucoptera* Gmelin), American white-winged crossbill. The first crossbill recorded in the Monument was the only one sighted in 1953. On July 29 I saw a single female in the top of a willow-birch thicket back of the ruined church at Kaguyak. The bird remained in view for less than a minute before it flew away through the trees, but the yellowish wash, wing bars, and even the crossed bill were distinguishable.

Crossbills were fairly numerous in the spruce forest east of Brooks River beginning about August 12, 1954. After Schaller’s initial observation on that date, I saw birds or heard them singing on August 14, 19, 23, and 31 and September 1. Apparently only the males were vocal; they perched in the tops of the spruces and trilled loudly and often. This habit was particularly notable on August 31, a fine, sunny, still day, when the songs came from all directions. The birds were seen to feed on spruce cones among the upper branches of the trees.

Passerculus sandwichensis (Gmelin), Savannah sparrow (race unknown). Specimens that Hine collected June 22 and July 8, 1917, near Katmai Bay were stated (1919, p. 484) to be *P. s. anthinus* (formerly *alaudinus*), the western Savannah sparrow. Schaller obtained a specimen in 1954 from the west shore of Grosvenor Lake, on the Bering Sea drainage, which was identified by Pitelka as “close to” the same race. A series collected at Kukak Bay by Ridgway in July 1899 is assigned by Gabrielson to the subspecies *anthinus*. (Gabrielson and Lincoln, 1959, p. 776.) However, the races of the Savannah sparrow are now poorly defined, and in this account no attempt will be made to assign the bird at Katmai to subspecies rank.

P. sandwichensis was the most abundant sparrow in the Monument. On the western slope it was rated as "numerous" or "abundant" on about one out of every three occasions when it was seen. My records were made between July 8 and September 3, 1953, and between July 5 and August 30, 1954. The species arrived in the area well ahead of these dates on which they were first mentioned in my notes. It seems likely that the last autumn migrants departed soon after the first of September, for I was in the area 10 days after the last date in 1953, and 6 weeks later in 1940, without seeing a Savannah sparrow.

West of the mountains the species was recorded at 10 localities: On the south shore of Naknek Lake at the western boundary of the Monument, August 17, 1954; near Brooks River, July 12, 1953, and August 1 and 30, 1954; 1 mile north of Brooks River, July 8, 1953; crest of Mount Dumlup, July 11, 1953; two localities on the shores of Iliuk Arm, July 16 and August 30, 1953, and August 2 and 21, 1954; Savanoski, August 24 and 27, 1953; lower American Creek, July 18, 1954; northeastern shore of Lake Coville, July 7, 1954; Grosvenor Lake at three localities, July 5, 12, and 22, 1954; and at the main fork of Kamishak River, September 3, 1953. Most of the areas were less than 200 feet above sea level, but the crest of Mount Dumlup was 2,400 feet in elevation.

On the Bering Sea slope Savannah sparrows were found in willow thickets or willow-alder-cottonwood seven times; in grassland (usually with some willow), six times; among birch-willow and scattered spruces, four times; and once each in a cottonwood grove and alder-fringed spruce. The species seemed to be rather partial to moist places, for it was often seen on the fringes of marshes. Two birds were caught in mouse traps that had been set along a small stream in a wet swale on otherwise dry tundra near the crest of Mount Dumlup. They were not saved, but Schaller preserved a male bird (his number 150) which he shot July 10, 1954, in an alder thicket on the west shore of Grosvenor Lake. The testes measured 4×1 and 3×1 mm.

Comparatively little time was available during the Katmai Project for field observations along Shelikof Strait, but I found Savannah sparrows at Kaguyak and on Kuikpalik Island, July 29, 1953, and in Hallo Bay, July 11, 1954. The species was "numerous" at the first two localities. It was living in birch-willow thickets near the ruined church at Kaguyak, on the open grassy flats of Kuikpalik Island, and in alder thickets that fringed the spruce forest in Hallo Bay. Farther south on the coast Hine found the Savannah sparrow common at Katmai Bay and referred to it as "a characteristic bird" of the region. As was mentioned previously, he took specimens here in the summer of 1917.

Junco hyemalis hyemalis (Linnaeus), northern slate-colored junco. The junco was fairly common throughout the lower elevations of the Monument on the Bering Sea drainage. I did not see it along Shelikof Strait, nor did Hine at Katmai and Kashvik Bays in 1917. The highest area where the junco was found (on Hardscrabble Creek) was 600 feet above sea level. The species was recorded early in July and as late as August 20, 1953, and August 31, 1954. I did not find it in the fall of 1940 (September 4-October 7), so apparently the migration occurs around September 1. The period of greatest abundance was mid-August.

A list of localities where the species was observed included the Brooks River area (nine occurrences); 1 mile north of Brooks River, and Lake Coville (three occurrences each); Savanoski area (two occurrences); and Hardscrabble Creek, Grosvenor Lake, east of Brooks Lake, and north shore of Naknek Lake (once each). The junco appeared to prefer spruce forest, sometimes with an understory or admixture of alder, willow, or birch, and I found it there 12 times out of a total of 19 occurrences when I recorded habitat descriptions. In addition to finding the species oftener in spruce stands than in all other habitats combined, I noticed that it was present there in greater abundance than in other vegetation types. The latter were: Willow or alder, or a mixture of the two (four occurrences); birch-willow (two occurrences); and cottonwood grove (once).

Some individuals, particularly those seen around the middle of August and presumably migrants, had a noticeable buffy cast on the back and side. Brody remarked on this characteristic in seven females and juveniles that he saw near Brooks River on August 18, 1954.

Neither Osgood nor Hine saw the slate-colored junco during their work in the region (1902 and 1917, respectively), but Gabrielson listed it among the species that he observed at Brooks Lake, July 9 and 10, 1946. He "saw two obviously mated pairs that scolded at him for some time." (Gabrielson and Lincoln, 1959, p. 781.)

Spizella arborea ochracea Brewster, western tree sparrow. This sparrow with the reddish-brown crown was fairly common and widely distributed in the Monument west of the Aleutian Range. I recorded it at least 25 times in my field notes for the two seasons of the Katmai Project, but saw it on numerous other occasions as well. The species was most numerous at low elevations, but I found one bird in tundra environment east of Murray Lake at an altitude of 2,050 feet where the few clumps of willows and alders were confined to sheltered

ravines and other depressions. The lateness of the season, September 5 (1953), suggested the possibility that this bird was a migrant and crossing country above the normal habitat.

The wide distribution of the species within Katmai Monument is indicated by the list of localities where it was observed, as well as number of occurrences: Brooks River locality (nine); Savanoski region (five); Lake Coville (three); Iliuk Arm (two); Murray Lake, Headwaters Creek, American Creek, and North Arm of Naknek Lake (one each). Birds were seen also along the western boundary of the Monument at two points—south of Naknek Lake and on the island in the middle of the same lake.

The tree sparrow is normally a bird of scattered thickets or clumps of trees in grassland. At Katmai I found it in this type of environment 21 out of 25 times. On only four occasions was it in unbroken woodland—twice in spruce forest and twice in cottonwood groves. The shrub-grassland or tree-grassland vegetation types in which it was seen were: Willow, usually pure but sometimes with cottonwood, alder, birch, or spruce (12 occurrences); alder, usually with willow and cottonwood-spruce (4 occurrences); spruce with willow and birch or alder (3 occurrences); and birch-willow (2 occurrences).

Tree sparrows were usually present singly or in pairs through the summer and early fall. I found them in larger numbers, sufficient to term the species "numerous" or "abundant," in the Savanoski region on August 16 and 20, 1953, along the northwestern shore of Lake Coville July 7, 1954, and in the Bay of Islands August 15, 1954.

Schaller discovered the dainty grass nest of a tree sparrow on the slope 100 yards north of Coville River, July 5, 1954. The nest was on the ground in moss, grass, and dwarf bunchberry, amid scattered clumps of scrub birch and willow. It contained three eggs which hatched July 18.

Tree sparrows were present in the area each year when we arrived at the end of June. The last dates on which I recorded its presence were September 1 (1954) and September 8 (1953). In the fall of 1940 I saw the species only once, on September 6. It is probable that the fall migration took place from mid-August through early September and that all the birds had left the area by the middle of the month.

Zonotrichia leucophrys gambelii (Nuttall), Gambel's white-crowned sparrow. From the beginning of our fieldwork in late June white-crowned sparrows were seen almost daily until August 20 (1953) and 31 (1954). From the fact that I did not see any birds during the

period September 4 to October 7, 1940, it may be inferred that the southward movement had cleared the Katmai region by early September.

White-crowns were recorded 12 times along and near Brooks River (July 12 and August 15, 1953; July 31, August 1, 14, 19, 20, 23, 31, 1954); four times at various points around Lake Coville (July 8, 9, 1954); three times each near Grosvenor Lake (July 5, 22, 1954) and at Savanoski (July 18, August 16, 19, 20, 1953); twice near Naknek Lake 1 mile north of Brooks River (July 7 and 14, 1953); and once each on the north shore of Naknek Lake (July 7, 1953), on Headwaters Creek (June 30, 1953), and at Kafia Bay (July 3, 1954). Gabrielson (Gabrielson and Lincoln, 1959, p. 790) also saw several birds at the outlet of Brooks Lake on July 19, 1940, and he recorded four at this place July 10, 1946. The species, therefore, ranged over the low country below 300 feet altitude on both sides of the mountains. Its ecological preferences, as expressed in numbers of sight observations in 1953 and 1954, were as follows: Willow thickets, sometimes with birch, cottonwood, spruce, or alder, eight occurrences; spruce forest, pure or with the hardwood species, seven occurrences; cottonwood groves, four occurrences; alder thickets, three occurrences; and birch (sometimes with willow, alder, cottonwood, or spruce), three occurrences. The largest concentrations of white-crowns were found in willow-birch thickets (around, and 2 miles west of, the outlet of Brooks River, July 7, 12, and 14, 1953), and in birch-willow with scattered spruces (on slopes west of Grosvenor Lake, July 5, 1954).

A nest containing three young that were beginning to acquire down was discovered on July 7, 1953, about 1 mile north of the outlet of Brooks River. The nest, made of dead grasses, was situated in a hummock of dry grass at the base of a *Potentilla* bush. The site was at the edge of a marsh where scattered scrub birches and willows pioneered from the surrounding woodland.

Juvenile white-crowns became numerous early in August, when the adults began to change into winter plumage. Brody noted that during the last week of August, 1954, adults and young of the season were present in the Brooks River area in approximately equal numbers.

Zonotrichia atricapilla (Gmelin), golden-crowned sparrow. One of the widest-ranging of the sparrows, the golden-crowned was generally uncommon in the Monument. I recorded it during each of my three visits, but the maximum number of occurrences (in 1954) was only six. Seasonally, it was seen as early as July 5 (1954) and as late as September 11 (1940).

Since most of our time was spent at low altitudes, a preponderance of the observations on this and numerous other species were made there. Below 400 feet I saw golden-crowned sparrows in two localities around Grosvenor Lake, July 5 and 22, 1954; near the south shore of Lake Coville, July 9, 1954; on the lower Ukak River, September 11, 1940; and at Brooks River, July 26, 1954. Gabrielson also recorded the species at the head of Brooks River, July 19, 1940, and July 9 and 10, 1946. Near sea level on Shelikof Strait Schaller saw a pair of golden-crowns in Kuliak Bay and one bird in Hallo Bay. Above the lowlands I found the bird "abundant" between 900 and 1,200 feet altitude north of Idavain Lake, August 29, 1954. An individual golden-crown was reported early in August, 1953, at 2,000 feet near the head of Knife Creek, and the highest bird recorded was caught July 11, 1953, in a snap trap at about 2,400 feet near the crest of Mount Dumlup.

Judging from Hine's comments, this species may have been more numerous and widely distributed in 1917 than it seemed to be during our work in the Monument about 35 years later. He stated (1919, pp. 484-485) that it was quite common "over much of the Alaskan territory visited." This presumably included Kashvik Bay, Katmai River valley and surrounding mountains, and the Ukak River valley and head of Iliuk Arm.

The concentration of golden-crowned sparrows near Idavain Lake on August 29, 1954, and the "flock" on Ukak River, September 11, 1940, were notable from the point of view of numbers and may have been groups of birds in migration. With these exceptions, I saw only singles or pairs and, in one instance, four birds together. Environmentally, this sparrow was equally attracted to tundra with alder-willow thickets in depressions, to cottonwood groves, and to alder fringes of lowland spruce forest.

Schaller collected two specimens, both on July 11, 1954. A female, which was given the field number 151, was taken in spruce-alder woods at the head of Kuliak Bay. The bird had small ova and an enlarged brood patch. The second specimen, a male with testes that measured 11 x 10 and 10 x 9 mm., was shot in very similar habitat in Hallo Bay.

Robert Johnsrud reported to me at the end of the 1953 field season that a golden-crowned sparrow stayed around the Project camp near the head of Knife Creek for five days in midsummer. It was quite tame and sometimes entered the tents, perhaps for crumbs of food or because other shelter was completely lacking in that desolate area. Then the bird vanished, and later was found dead in one of the tents.

Passerella iliaca unalaschcensis (Gmelin), Shumagin fox sparrow. Fox sparrows are found in Katmai National Monument on both sides of the Aleutian Range. The following account of our observations is included under only one geographic race, on the basis of a specimen taken by Hine in the Katmai River Valley which proved to be *P. i. unalaschcensis*. It is quite possible, however, that the fox sparrows on the Bering Sea drainage will be assigned to a different race when specimens become available. An individual that I saw at close range near Brooks River on August 22, 1954, was extremely reddish in color. This corresponds with the outstanding plumage character of *P. i. zaboria* Oberholser.

The bird at Brooks River was the only fox sparrow that I saw in the Monument. It was quite fearless and foraged on the ground near our tents in cottonwood–willow–spruce woodland. Schaller saw another bird, or the same individual, in a willow thicket near Brooks River about one-quarter mile away on the same day. He noticed a few more during the next three or four days. Less than a week later, on August 27, I found fox sparrows common among the alder thickets along McNeil River, about 20 miles northwest of the Monument on Kamishak Bay.

Gabrielson recorded the species near the outlet of Brooks River, July 9, 1946. Hine (1919, pp. 485-486) saw fox sparrows in woodland margins in the Katmai River Valley and collected a specimen July 9, 1917. Earlier, on July 1, 1899, Ridgway took an adult male in Kukak Bay. (Gabrielson and Lincoln, 1959, p. 798.)

Melospiza melodia (presumably *sanaka* McGregor), Aleutian song sparrow. A song sparrow collected by Hine, July 25, 1917, at Katmai Bay and assigned to the race *M. m. sanaka* (1919, p. 485) is the basis for the name used here. Hine's specimen, however, is the only one of its race that has been recorded east of Stepanovak Bay, some 200 miles away from Katmai Monument near the end of the Alaska Peninsula. On the other hand Bischoff's song sparrow, *M. m. insignis* Baird, is fairly common on Kodiak and adjacent islands—within flight range of the bird across Shelikof Strait. It is possible that collecting will show two races in the Monument, one on either side of the Aleutian Range.

Song sparrows were uncommon within our area. We saw none in 1954 and I observed only a few individuals during the preceding year. One was in scattered willow clumps near the outlet of Brooks River, July 12, 1953; another was seen near the same spot a month later, on

August 15. Three or four birds were flushed July 16 from the scattered willows on the small islands in Iliuk Arm near the mouth of Margot Creek and a few were seen the following day in alder-willow thickets around our camp site at Savanoski. On Shelikof Strait, one song sparrow was seen as it skulked among some scrub willows on Cape Douglas, July 29, and another lone bird was found among alders northeast of the cannery in Kukak Bay on August 3, 1953. The only 1940 record of the species in the Monument consisted of two birds that I saw on October 7 as they flitted about among the buildings of the same cannery in Kukak Bay. In 1917 Hine observed "a few specimens . . . along the rocky coast of Katmai Bay."

Calcarius lapponicus alascensis Ridgway, Alaska Lapland longspur. This is a tundra-dwelling species which at Katmai has not been recorded below the 1,000-foot elevation.

On August 17, 1953, I found many longspurs feeding busily through the short, brown grass on the rolling hills between the north shore of Naknek Lake (North Arm) and Idavain Lake at about 1,000 feet altitude. The birds were with numerous western water pipits. A little over a year later, on August 29, 1954, large flocks of both species were seen in similar but even higher terrain (1,200 to 2,000 feet above sea level) a few miles north of Idavain Lake. (See p. 138.) Brody, who was with me, estimated a total of 150 longspurs were seen in about 3 hours. Schaller made a separate excursion in the region at the same time and reported finding several large flocks of from 50 to 300 birds.

Osgood (1904, p. 74) saw Alaska longspurs daily at various points along Becharof Lake in mid-October, 1902. He noted several at Puale Bay as late as October 25. Hine (1919, p. 484) found nesting longspurs plentiful in the tundra on the mountains around Katmai River Valley in the summer of 1917. He obtained specimens in breeding plumage on July 12, and "other specimens" on August 15.

Plectrophenax nivalis nivalis (Linnaeus), eastern snow bunting. A hiker in the Valley of Ten Thousand Smokes encounters this species with surprising frequency considering the desolation and utter absence of vegetation over wide areas. In comparison with other birds, the snow bunting is by far the most numerous. It also impresses the visitor as being the only bird that is thoroughly "at home" and foraging successfully amid the burned-out fumaroles and expanses of pallid, barren pumice. To the best of our knowledge, it is the only avian

species that nests and rears young in those areas that have been thoroughly devastated by volcanic forces.

Hine and other members of the National Geographic Society expedition of 1917 saw "snowflakes" on several occasions in upper Katmai Canyon, and a pair was seen and heard singing on upper Mageik Creek (Hine, 1919, p. 476). At the time, practically no green vegetation existed in those areas, although insects were abundant at times.

By 1953-1954 it was not unusual to see three to five or even more individuals of this species in a half-day's walk over the upper portion of the Valley of Ten Thousand Smokes. On July 21, 1953, I counted four buntings during a hike of five hours across the head of Knife Creek Valley. Two were seen August 7, 1954, in a short time on the south fork of Knife Creek. Three days previously Schaller had recorded five birds in the upper valley of Knife Creek. Buntings were most numerous near streams in the valley and along the fronts of the Knife Creek Glaciers at the western base of Mount Katmai.

Here, just outside of an ice cave in the glacier front which served as the principal feeder for the south fork of Knife Creek, I watched a snow bunting on July 21, 1953. The bird flitted and darted about erratically, evidently catching insects. At one point the bird stopped and vigorously worried an object which was about the size of a large dragonfly but appeared to be composed of a tangle of fibers. Because of the intervening torrent of water, it was impossible to move closer and determine the identity of the object.

Curtis (personal communication of April 25, 1955) reported finding a nest of this species in a hole in the bank of Knife Creek about one-half mile below the junction of the north and south forks. The depression was in the pumice outwash from the north slope of Broken Mountain and was about 2 feet deep. As the tunnel ran partially under a ledge, it was impossible to obtain a clear view of the nest at the bottom. However, Curtis was sure that at the time, July 2, 1954, at least three eggs were present. Later, on July 17, he was able to determine that four young were in the nest. Passing again on July 22, he noticed a young bird in the entrance to the tunnel. The nestling, on seeing him, scrambled back in fear. Curtis was uncertain whether any of the brood had flown.

In more normal environment snow buntings live in the tundra zone on the high mountains. Johnsrud and Kistler saw several birds of this species, July 22, 1953, at 2,000 feet altitude on an east-west ridge of Mount Kejulik. This area was a relatively short distance

outside of the south boundary of the Monument and west of Kejulik River. Schaller was surprised, after climbing to the summit of Knife Peak on August 5, 1954, to find three snow buntings foraging through the sparse grass. This established a maximum altitude for a ground-feeding bird species in the Monument, as Knife Peak is the highest elevation—7,589 feet above sea level.

Osgood saw a small flock of snow buntings near Becharof Lake on October 6, 1902. If these birds were near the lake itself, which is under 50 feet in elevation, they were at the lowest altitude for which we have a summer-fall record in the Katmai region. Osgood (1904, pp. 73-74) added that the species "also breeds at Cold (now Puale) Bay, where Maddren found it nesting in high rocky cliffs in the summer of 1903." Hine and other members of the National Geographic Society parties observed "snowflakes" on mountain tops within the Monument.

HYPOTHETICAL LIST

Gavia adamsii (Gray), yellow-billed loon. Osgood (1904, p. 51) recorded a large loon, "either this species or *G. immer*," that was killed and eaten by natives at Cold Bay (now Puale Bay), October 17, 1902. The locality is only 18 miles west of the Monument boundary, and the coast is very similar ecologically to that in the southern part of our area.

Branta nigricans (Lawrence), black brant. I saw a flock of a dozen geese, probably belonging to this species, over the outlet of Savanoski River on August 30, 1953. A number of larger groups were observed in the same area between September 23 and 26, 1940. One of the latter flocks made a close approach, but the others were flying at a considerable height and apparently were bound for Cook Inlet. Because positive identification was not made in any of these instances, the species is listed as "hypothetical."

Anser albifrons frontalis Baird, white-fronted goose. My only observation of (apparently) this species was made August 19, 1953, when I saw a flock of seven birds fly over the mouth of Savanoski River and on up the valley. Positive identification was not made.

Bucephala albeola (Linnaeus), bufflehead. Two or three ducks, believed to have been buffleheads, were seen at a distance July 15, 1953, on the circular pond about one-quarter mile east of the mouth of

Brooks River. Because of the uncertainty of identification and the absence of any other record for the Monument area (particularly the area west of the Aleutian Range), the species is placed in the hypothetical list.

The only positive record of buffleheads in the region is that by Wilfred H. Osgood (1904, p. 57). On October 17, 1902, he saw two birds that had been killed by natives on Cold Bay (now Puale Bay), about 18 miles west of the present Monument boundary.

Somateria mollissima v. nigra Bonaparte, Pacific common eider. Good-sized flocks were seen by Osgood on Becharof Lake where he collected a young male in transition plumage on October 7, 1902. He also saw large flocks at Puale Bay. Both bodies of water are within 20 miles of the western boundary of the Monument, the adjacent region of which contains very similar aquatic habitats and shorelines. Species that frequent the two areas mentioned in Osgood's account (1904, p. 58) are almost certain to be recorded eventually within the Monument.

Limosa fedoa (Linnaeus), marbled godwit. Brody identified a single marbled godwit on the mud flats of the tidal lagoon at the mouth of McNeil River on August 27, 1954. The area is 23 miles northwest of the Monument boundary but is so similar ecologically to coastal areas in the Douglas River region as well as Shelikof Strait that the species undoubtedly will be recorded eventually within the Monument.

Phalaropus fulicarius (Linnaeus), red phalarope. A phalarope, believed to be of this species, was seen by Osgood (1904, p. 61) October 6, 1902, on Becharof Lake. We have no positive record for the Monument.

Nyctea scandiaca (Linnaeus), snowy owl. This species is a regular winter visitor to regions around the Monument, including Naknek and Becharof Lake. Its absence from the confirmed list of birds undoubtedly is due to an utter lack of observations within our boundaries at the proper season.

IV. THE MAMMALS

REMARKS AND ACKNOWLEDGMENTS

Unlike birds, most mammals are nocturnal, secretive, and difficult to see. The presence of many species can be determined only by trap-

ping individual animals or by careful and time-consuming search for signs of their passing. Certain mammals, particularly the smaller carnivores, leave so little trace of their presence that tracking snow is almost essential for their study. As the Katmai Project was limited to summer and early fall seasons, portions of this report on the mammals of the Monument are deficient in details.

Time did not permit me to trap and prepare specimens, but some of this work was done by Everett L. Schiller in connection with his studies of mammalian occurrence and distribution in Alaska and of animal-borne diseases (Schiller and Rausch, 1956). Some information from this source has been included. Other personnel of the Project assisted by describing field observations of mammals which came to their attention. Credit is given for each of these contributions in the accounts of species that follow.

Most of the nomenclature in this section of the report is based on Palmer's "The Mammal Guide," and on Hall and Kelson's "The Mammals of North America." I am especially grateful to Dr. E. Raymond Hall for his advice in this field and for information from his manuscript prior to its publication.

ANNOTATED LIST

Sorex vagrans shumaginensis (Merriam), Dusky Shrew

S. cinereus hollisteri Jackson, Common Shrew

S. arcticus tundrensis (Merriam), Tundra Shrew

All three of these shrews have been recorded from the eastern portion of the Alaska Peninsula. A number of specimens of the first two species were taken by Schiller (Schiller and Rausch, 1956, p. 193) in Katmai National Monument. *S. arcticus* is assumed to be present since it was found (sparingly) by Osgood on his trip across the Peninsula west of the present Monument in 1902.

Dusky shrews were trapped in three habitats in the western portion of the Monument and at one area on Shelikof Strait. Although nowhere abundant, the species was most numerous in a very wet sedge marsh (pl. 3, fig. 2) near the south shore of Naknek Lake about 2 miles north of Brooks River. Two common shrews also were captured in this marsh. A few dusky shrews were found in the spruce-cottonwood-birch-alder woodland nearby, at an elevation of about 100 feet. In both the marsh and woodland the shrews were associated with meadow mice (*Microtus oeconomus kadiacensis*). Both of these small



1. A Pacific golden plover searching for insects in the mud beside a small stream near Savanoski Village site, August 20, 1953.



2. Young short-billed mew gulls in a small nesting colony at Kukak Bay. The species was common, but much less numerous than the glaucous-winged gull. July 25, 1953.



1. A crude boat frame which had been made by an Eskimo hunter to transport the meat and hide of a brown bear that he had killed. The frame, made on the spot from alder poles, was covered by the hide. (See pp. 176-177.) Photographed at Brooks River about September 10, 1940.



2. Brooks River is noted for its steelhead angling as well as for runs of red salmon. Brown bears that come to the stream for salmon may conflict directly as well as indirectly with human fishermen, both white and Eskimo. (See p. 182.) Photographed July 2, 1953.



1. For generations Eskimo have utilized the red salmon of the Naknek River drainage. A choice seining place is near the outlet of Brooks River into Naknek Lake. This youngster from "new" Savanoski was hanging fish to dry for winter use. (See p. 174.) September 6, 1940.



2. Brown bears step in the footprints of preceding individuals. In the deep mat of tundra vegetation, footprints may be 6 inches deep. This trail along the south shore of Kulik Lake had been used for many years. (See pp. 170-171.) September 3, 1953.



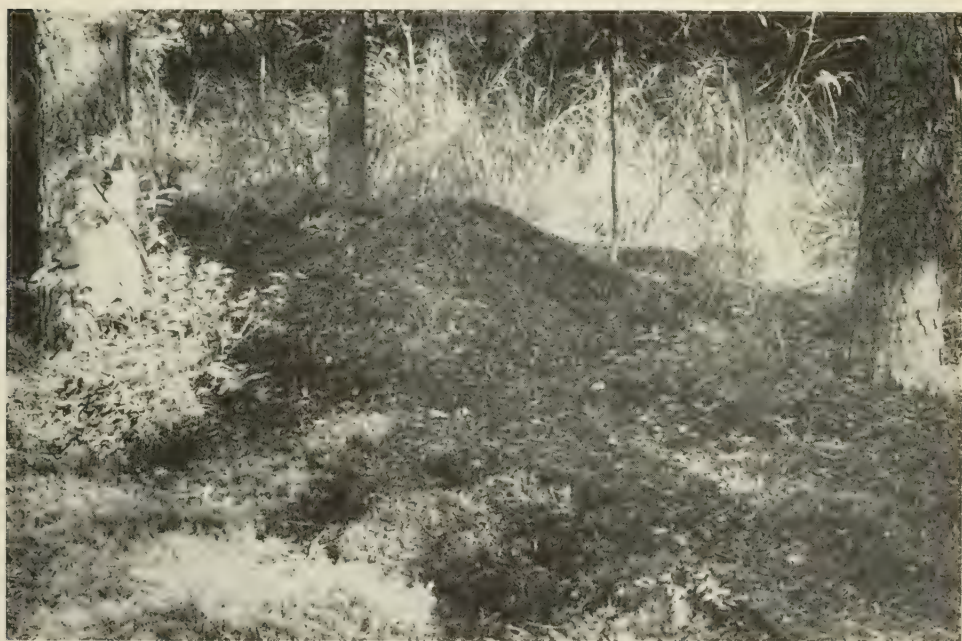
1. Salmon are extremely important in the brown bear's diet. This animal on the bank of O'Neil River is tearing at a freshly caught fish, while glaucous-winged gulls wait impatiently for the leavings. (See pp. 167-169, 173-174.) Photograph by Gerald L. Brody, August 26, 1954.



2. A mother otter leading her three young swimming around a rocky island in northwestern Iliuk Arm, September 12, 1953. (See p. 189.)



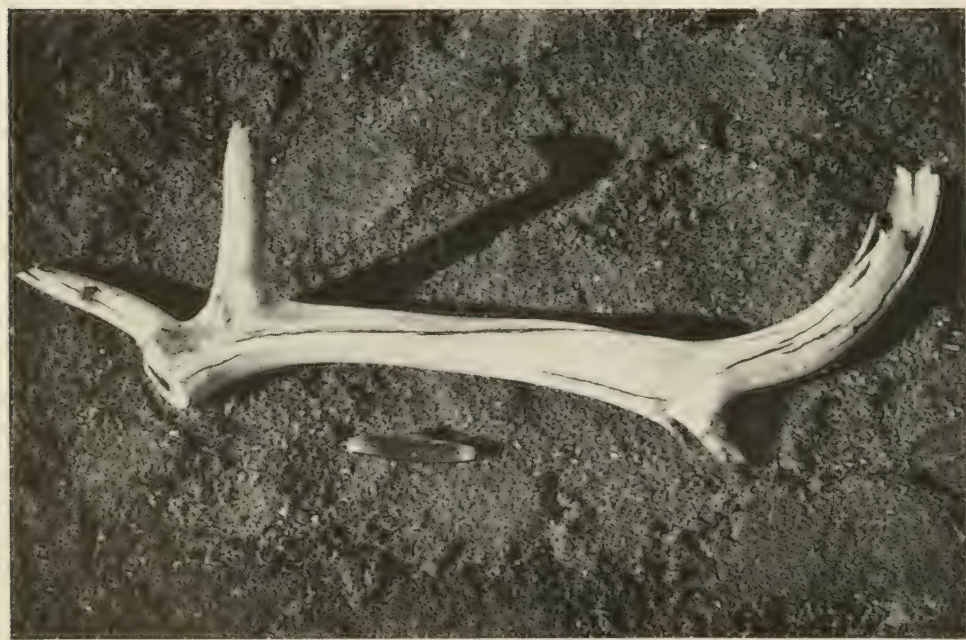
1. Red foxes were numerous in the Katmai region during the survey. This mother fox reared a family of 6 in a den only 50 feet from the archeologists' diggings near Kukak Point in Kukak Bay. (See pp. 191-192.) August 2, 1953.



2. Food midden and feeding station of the red squirrel in the white-spruce forest east of Brooks River. This pile of bracts and other parts of spruce cones, discarded after extraction of the seeds, was about 2 feet deep. (See p. 203.) August 1, 1954.



1. A violent flood may have contributed to the drastic reduction in the beaver population on Hardscrabble Creek during 1952-53. Dams were broken and lodges deserted. (See p. 205.) The unusually large beaver lodge was photographed August 19, 1953.



2. Grant's caribou disappeared from Katmai probably before 1920, and the subsequently introduced Kamchatka reindeer by 1942. Networks of trails, perhaps made by caribou and Old World deer, were still discernible on the tundra in 1953. This weathered antler was found near Sugarloaf Mountain, August 17, 1953. (See p. 228.)

mammals were scarce in 1953, but in the woodland shrews apparently outnumbered meadow mice by about two to one.

A few dusky shrews were captured beside a streamlet in a small swale which was surrounded by typical tundra near the summit of Mount Dumlup. The only other small mammal taken in this habitat was one jumping mouse (*Zapus hudsonius alascensis*). The elevation was 2,400 feet—the highest altitude at which shrews have been recorded in the Monument.

Dusky shrews were found in moderate numbers at the abandoned cannery in Kukak Bay late in July, 1953. Here they had an abundant food supply in the extraordinarily large population of red-backed mice (*Clethrionomys rutilus dawsoni*). The vegetation was *Calamagrostis* grass, *Equisetum*, and fireweed, with clumps of alder, willow, and red-berried elder. On the sandy ridgetop between Kukak and Kafia Bays, at an altitude of 2,000 feet, I saw small runways and tunnels that appeared to have been made by *Sorex*.

Two common shrews (*S. cinereus*) were trapped by Schiller in mid-July, 1953, among the grasses and *Equisetum* on the bank of a small stream near our camp at Savanoski. The next season, on June 30, I saw a shrew in the same place; it presumably belonged to this species.

To summarize: Shrews were uncommon to fairly common in the Monument in 1953, with the dusky shrew (*S. vagrans*) being much more numerous than the common shrew (*S. cinereus*). The latter apparently was limited to low elevations west of the Aleutian Mountains, while the dusky shrew occurred from sea level to 2,400 feet on both sides of the Range.

Myotis lucifugus lucifugus (Le Conte), Little Brown Bat

The species has been reported on Kodiak Island (Miller and Allen, 1928, p. 45) and at Iliamna Village (Osgood, 1904, p. 50).

In particularly favorable localities this small bat is present during the summer months. The earliest record of the species was made on July 8 (1954), when I saw a single animal fly over our camp in a cottonwood-spruce grove on the spit between Lake Coville and the north shore of Coville River. The latest date in fall was about September 5 (1940), when one or more bats flew within range of the cabin lights of our boat which was tied up to the bank of Brooks River about 200 feet from Naknek Lake. The evening, like the preceding daylight hours, was still and unseasonably warm and humid. These

conditions were favorable for insects to move about, and the bats took advantage of the food.

Under very similar conditions, at least three bats were seen between 10 p.m. and midnight on July 7, 1954, swooping repeatedly over and parallel to the sandy beach on the Coville River side of the spit mentioned above. As the insects were venturing out of the woodland understory into the open, the bats were taking them in repeated passes about 100 feet in length.

Single bats were seen on two or three evenings between July 16 and 20, 1953, over our camp at Savanoski. This site was on a sandy flat through which a small stream flowed into the Savanoski River. Back of the flat was an extensive damp woodland of spruce, cottonwood, alder, and willow. Insect life was notably abundant. Later the same summer a very few bats were seen hunting along the edge of the cottonwoods on the south shore of Naknek Lake north of the outlet of Brooks River.

The little brown bat is uncommon in the Katmai area. Undoubtedly it is limited to the lower elevations in and near woodlands.

Ursus gyas Merriam, Peninsula Brown Bear

The brown bear is the world's largest carnivore, and the Peninsula brown bear is the largest member of the group. Katmai National Monument provides optimum habitat for the Peninsula brownie and is in fact this bear's only year-long sanctuary. The area therefore has a special significance in the protection program for America's wildlife.

Physical and sensory characteristics.—Precise information on the weight of the Peninsula brown bear is difficult to obtain under field conditions. Presumably no bear from the Monument has been weighed. It can only be estimated, therefore, that an exceptionally large male may approach 1,500 pounds. The imprint of the hind foot of a medium-size bear that crossed the Valley of Ten Thousand Smokes in July 1954 measured 10 inches in length. Two large bears made tracks (of the hind foot) which measured 12½ inches (north-western shore of Grosvenor Lake, July 5, 1954) and 13 inches (west shore of Iliuk Arm, July 1, 1953). Although the record was confused by the tracks of other bears, the last animal appeared to have been accompanied by a cub. If this was correct, the bear with a 13-inch hind foot was an exceptionally large female.

The tremendous strength of the adult brown bear is illustrated by

the following incident. Early in July, 1954, the decomposing carcass of an adult cow moose drifted into the mouth of Coville River. The teeth indicated that the animal had been past the prime of life and had probably succumbed to winter-kill a few months previously. Schaller and I towed the carcass through the river and grounded it on the northwest shore of Grosvenor Lake near a clump of spruces. Desiring to use the dead moose as bait for photographs, we attached ropes to the feet and tried to pull it out of the water. Although the viscera were missing, our combined efforts were insufficient to move the weight more than a couple of inches further in the shallows. The following night a bear pulled the carcass completely clear of the water and, apparently without feeding, covered it with gravel.

On the next evening Schaller climbed into the largest spruce about 20 feet from the cache. Although the light soon faded too much for photography, observation was still possible and the man stayed at his post. He was rewarded about midnight when a medium-size bear appeared. Walking up to the carcass, the bear grasped a hind leg in its mouth. With what appeared to be a sideways twitch of its head, the bear jerked the heavy carcass out of the gravel that covered it! The movement was made so quickly and with so little apparent effort that the observer was astounded.

The brown bear has three gaits. Most travel is performed at a deliberate, evenly paced walk. Although it appears effortless and leisurely, it carries the animal over soft or uneven ground and through dense, tall grass at a rate that probably exceeds 3 miles per hour. In the same type of footing a man cannot walk at this pace for more than a couple of hundred yards before being exhausted. Yet the bear can traverse hills and valleys where the ground is spongy, sprinkled with frost pits and hummocks, and covered with a tangle of dwarf shrubs and other plants, with an easy indifference that excites admiration in the human onlooker.

The second gait is a quick, flat-footed shuffle that the animal uses for a few yards, such as when fishing or maneuvering around an opponent. The feet may move independently or the pair on either side may be advanced simultaneously. The result is a darting movement with little or no up-and-down motion of the head and body. The shuffling run is never used for any distance. If the animal wishes to continue rapidly, it breaks into a third movement—the gallop.

Except when the adult brown bear may lunge briefly on a steep slope to maintain its balance, it gallops only in emergencies. The rear legs move together, sending the animal forward in powerful bounds, while

the front feet land well apart with one somewhat ahead of the other. In spurts of maximum speed, the hind feet may be advanced up to or even ahead of the position of the front feet, somewhat as the rabbit runs but not as exaggerated. The gait is bouncy, with the gathered, compacted body rising and falling as much as a foot above and below a median horizontal line. As a thoroughly frightened bear puts on a supreme burst of speed, the bounding motion tends to flatten out, but this maximum effort is never maintained for more than a short distance.

The gallop may be performed in a partially sideways position with the body directed 20 or 30 degrees away from the direction of travel. Usually this angle is assumed to permit the animal to look to the rear at a real or fancied pursuer. I cannot even guess at the speed with which the brown bear can gallop. In the rough, tangled footing of its native environment, the animal certainly could overtake a fleeing man very quickly. The gallop, if not forced, can be maintained for a considerable distance. I have seen adult and yearling bears bound through grass several feet tall for more than a mile, with no evidence of slowing down as they disappeared from view.

For an animal of its bulk, the brown bear displays great agility and considerable dexterity. Its success in leaping on salmon in rapids and riffles of streams is testimony to its speed and quickness, for an alert salmon can move almost faster than the human eye can follow. The bear clammers about on steep slopes and climbs up and down past overhanging banks with apparent clumsiness but actually with considerable dexterity. Several bears demonstrated their skill in climbing around on a rock cliff about a mile north of Brooks River in early July, 1953. The carcass of a bull moose was wedged in the broken rocks at the water's edge near the base of the bluff, and the bears visited the spot at frequent intervals to feed. Their much-branched trails went over the 20- to 30-foot cliff in two or three places. One stretch of nearly 6 feet was almost vertical. In such climbing the long claws were highly useful and the rocks above the moose carcass were much scuffed and scratched.

In addition to being strong and dextrous climbers brown bears are either venturesome or oblivious to the hazards of high places. On July 28, 1953, I saw a number of trails which had been made by individual bears as they crossed the steep pumice slopes on the mountains behind Dakavak Bay. Tracks made in this material persist until they are obliterated by strong winds and are visible for a considerable distance. At the greatest angle of repose a creature as heavy as a bear sinks

and slides in the unstable "sand," and even for a human progress is slow and uncertain. Nevertheless, two or three times bears had walked across very steep slopes which terminated in sheer rock cliffs 400 to 500 feet high. A fatal fall, or at best entrapment, would have resulted from sliding or falling on some of these pumice slopes.

It appears from the following observation that the animals ignore or are unaware of objects, even those close by, unless scent or hearing bring information as to their character. Near the south shore of Kulik Lake, about 2 miles east of the western end, a very conspicuous bear trail ran parallel to the water's edge. Many footprints were worn as much as 5 inches deep. Evidently the trail had been made by many years of use and was a "highway" along this long lake. In crossing an open, grassy slope the bears' direction of travel passed through an isolated glacial erratic. The boulder was fully 6 feet in height and of about the same diameter, and was all the more conspicuous because it was the only stone of appreciable size in the vicinity. Nevertheless, the trail showed plainly that each bear walked to within 2 feet of the boulder, turned and circled around one side, and resumed the original direction of travel at a point almost directly opposite the spot where the detour commenced. It was apparent that the animals made no attempt to anticipate their arrival at the obstacle, but plodded on until almost touching it before turning around the downhill side.

From the above one may infer that the brown bear's sight is poor. Either this is true or the animal is habitually indifferent or inattentive to its surroundings. It does seem to have good perception for moving objects, as is shown in the following incident. Three of us posted ourselves (August 26, 1954) on a 50-foot bluff above O'Neil River (about 25 miles northwest of the Monument) in order to obtain pictures of bears as they fished for salmon about 300 feet distant. Noise made by the rushing water was sufficient to cover any ordinary sounds of our activity. As long as we were motionless when the animals looked in our direction, we were undetected. Eventually, however, we became less cautious and the bears found us immediately. A little later, under similar circumstances, I was seen by two bears which rushed off in a great fright as soon as I moved on the skyline.

If the brown bear is not alarmed, it manifests a strong curiosity toward unidentified objects or actions that are foreign to its experience. A folded canvas boat that was left over the winter of 1953-1954 on the southwestern shore of Grosvenor Lake was pawed over and ripped by a bear that found it, probably after coming out of hibernation. The boat had never been set up, so it was not odorous of food

and probably carried little or no man scent. It had not been mauled about, as an angry bear would have "savaged" it. Its appearance suggested that the animal had investigated the package out of curiosity. In another instance (which has been cited also on page 159), a bear feeding at a carcass apparently caught the scent of a man who was perched in a tree about 12 feet above the ground. The bear paced nervously back and forth several times, then walked to a point about 12 feet from the base of the tree and stared fixedly upward. Because of dim light the animal apparently was unable to determine that the object in the tree was a human. After what seemed to the man a long time, the bear looked away, then went off a short distance and probably went to sleep. In a third instance a bear was said to have spent some time on several successive days in June 1953 watching two biologists who were recording data at the salmon-counting weir near the Brooks Lake fisheries laboratory. The actions of the animal were interpreted by Dr. Charles Hunter, who described the occurrence to me, as manifesting curiosity.

The characteristics of aggressiveness and timidity, which are displayed at times, will be discussed under the heading, "Relations with Man" (pp. 176-185).

Distribution and numbers.—It is difficult to find a sizeable habitable area in the Monument where at least one bear has not been at some time during the spring, summer, or fall. Even the sterile "sand flow" in the Valley of Ten Thousand Smokes and the lower portions of snowfields cannot be excepted, for lone animals occasionally wander across them. Bears sometimes move onto the open tundra, either to hunt ground squirrels or to cross ridges, but this seems to be rare during the warmer months (June through September). Through this period practically all the bears live at elevations under 1,000 feet. In fact, few of them climb much above 500 feet while salmon are readily available in the lower streams. This means that on the Bering Sea drainage within the Monument most of the bear population is found in an altitudinal range of little more than 300 feet for at least half of the animals' period of seasonal activity.

The brown bear seems to range indiscriminately through most of the lowland habitats. During June, July, and much of August the animal lives largely on salmon and herbs (mostly grass). As the latter occur in abundance in the valleys near streams, there is no occasion for traveling far. Any growth that provides partial cover is acceptable as a living area, and most bears probably stay within one-quarter mile of a salmon stream for weeks consecutively. My notes indicate that,

back of the stream banks, bear sign was most frequently seen in alder or alder-willow thickets, in mixed grass and shrubs, and in mixed spruce-hardwood forest. Well-beaten trails ran through the unbroken spruce woodland such as that southeast of Brooks River, but it appeared that here the animals were mostly traveling rather than foraging and resting. Signs showed that some of the small grassy islands in southern Iliuk Arm had been utilized, perhaps in search of gull nests, but this habitat was insignificant in the entire picture. I found that the bears at Katmai would sometimes cross open marshes and bogs, and the great open delta of Ukak River, but these were merely areas used in transit. In summer the only openings where bears could be found regularly away from cover were the gravel bars along salmon streams.

Based on signs such as trails, food remnants, and droppings, as well as sight records of the animals, the areas west of the Aleutian Range most frequented in summer were as follows: Savanoski River from the outlet to a point 1 or 2 miles above Rainbow River, including the valley south of the Savanoski; southern shores of Naknek Lake and Iliuk Arm from the northeastern base of Mount Dumlplng east to the Ukak River (particularly the general area of Brooks River, the region east of Brooks Lake, the mouth of Margot Creek, and the northeastern lower slopes of Mount Katolinat); numerous areas around Grosvenor Lake, particularly the outlet of the lake and lower Hardscrabble Creek; American Creek above the marshes; and Douglas River. Along Shelikof Strait bears were most abundant in 1953 at the foot of the mountains from Katmai Bay north to Hallo Bay, with the greatest numbers appearing to be on the northern half of this coast (Kukak and Hallo Bays); and along Alagogshak Creek. Areas of scarcity (below 500 feet elevation) included the western and southwestern portion of Mount LaGorce, Takayoto Creek, and the region between Idavain Lake and Lake Coville.

By middle or late August the bears seemed to tire of their steady diet of salmon. This is suggested not only by their often half-hearted actions while fishing but by the comparative scarcity of bears along the streams after that time. Most of the animals left the vicinity of Brooks River before the end of August in both 1953 and 1954, although the stream below the falls was still thronged with red salmon. Careful observations along the lower Savanoski River from August 16 to 19, 1953, revealed that this portion of the watercourse had been deserted by the numerous bears that had frequented it throughout the previous month. In this case, however, the animals had moved up-

stream to the vicinity of the outlet of Rainbow River. We counted 23 in that area on August 19.

It is impossible to make even a rough estimate of the population of bears in Katmai National Monument. The most favorable time for making a census is July, when the species as a whole is concentrated on the salmon streams. Even then, however, the difficulties are numerous. Dense vegetation crowds in along all except the largest rivers, hiding the animals much of the time. Individual bears come to fish at different periods of the day or night, depending on natural preferences, size of the previous meal, and fear of competitors on the fishing grounds. The bears sometimes are identifiable by size, color, and other characteristics, but in a large population these peculiarities often are not sufficiently pronounced for certain identification. Bears on Kodiak Island have been marked with color, but this has not proved practicable on a large scale.

The haphazard tallies of bears that have been made in the Monument are interesting, although they are not very significant in forming an estimate of the total population. The largest count that I made was 23 bears along 10 miles of the Savanoski River, west of Rainbow River, on August 19, 1953. Ten bears were seen August 24, 1953, on the mud flats of the north side of the valley back of Hallo Bay. These counts are dwarfed, however, by one that was described to me on September 7, 1954, by a bush pilot, George R. Tibbetts of Naknek. While flying down the valley of Savanoski River about a week previously, he saw a total of 60 bears. If this count is reliable, it is possible that the total number of brown bears in the Monument approaches or even exceeds 200.

It was my impression that bears were less abundant in the summers of 1953-1954 than at the time of my first visit to Katmai in the fall of 1940. This impression was strengthened by the fact that they should appear more numerous in the summer season when the animals are concentrated along the salmon waters. Two local observers, John Walatka, manager of the public camp at Brooks River, and Jay Hammond, formerly warden of the Alaska Game Commission at Naknek, expressed the view that bears had indeed declined somewhat in numbers prior to 1953.

Among my notes that lend support to this conclusion are observations on travel routes in the region of Brooks River. A bear trail on the moraine between Naknek Lake and Iliuk Arm was examined on August 14, 1954. Its hard-packed surface and sharply defined sides indicated that it had been formed over a period of years, but no indi-

cations of use by bears during the current season could be found. Another trail that paralleled the east shore of Brooks Lake, 50 to 200 feet from the water, was found August 31, 1954. Beaten into the ground as deeply as 4 inches, it must have been a bear "highway" for many years. The path, however, was covered by moss which was unbroken by the long claws of bears. No recent sign was in the vicinity. It was evident that this route, which had formerly led to Brooks River and its abundant fish supply, had been abandoned.

Abandonment of old travel routes may result from a shift of population as well as an over-all reduction in numbers. A marked, but possibly temporary, exodus of bears from the Brooks River area was evident during the last week of August, 1954. Based on recent sign, particularly the remains of salmon left by bears near the river, less than one-quarter of the number of animals were patronizing the stream as compared with the same period of 1953. The salmon run, however, appeared to be virtually undiminished.

Another change of a similar nature may have occurred in 1954 along the coast of Shelikof Strait. As mentioned previously (p. 163), most of the harbors between Katmai and Hallo Bays had a good population of bears in July-August, 1953. Messrs. Samuel Keller and Hillard N. Reiser of the Geological Survey, who were alert observers, carried out two weeks of geological reconnaissance in this section of the Monument in August of the following year. During these two weeks they saw *one* bear. No explanation can be advanced except the possibility that greatly increased activity by commercial fishermen may have caused the bears to retreat back from the shores and the lower courses of salmon streams.

Habits.—The brown bear may be active at any hour, although the evening and early morning are the favorite times for food-gathering. This is compatible with the schedules of other animals which dwell in high latitudes, where the length of daylight and darkness vary seasonally. The bear sleeps, of course, through the winter months, but during midsummer it must adapt itself to almost continuous light. It seems probable that hunger is the principal activator that sends the bear abroad at odd times, modifying the normal schedule which avoids the midday and middle-of-the-night periods. Smaller and more timid brownies may come to the salmon streams when these places are not crowded by competitors for food. The sun's heat probably induces drowsiness in well-fed bears, causing them to stay out of sight from midmorning to about 5 p.m. A decrease in activity about four hours later, which lasts until 3 or 4 a.m., may be a period of digestion. The

fact that brown bears can move about in the dark without much visual difficulty indicates that they do not "lay up" during the middle of the night because of lack of light.

The brown bear is quite omnivorous. Even in July and early August, when salmon made up a large percentage of the diet by bulk, the bears were found to partake of many other items. During the first half of July, 1953, bears fed extensively on the carcass of a bull moose that had lodged in the rocks on the southeastern shore of Naknek Lake east of Mount Dumlup. (During the same period the following year, however, a bear near our camp on Coville River showed little appetite for the same kind of food.) Near Brooks River, on July 4, 1953, one of our party found a dropping that contained the undigested portion of the diaphragm of a large mammal, possibly a moose. On July 16, 1953, I watched a bear walk from a stream, where salmon were available, to feed on a mass of common horsetail (*Equisetum arvense*). The animal cropped the plants steadily, feeding along like a cow or horse, taking the material in without discriminating or selecting. The plants were eaten down to a height of 2 or 3 inches above the ground. During the last week of July and the first week of August the bears at Katmai turned for "salad" to the seacoast angelica (*Angelica lucida*) (pl. 6, fig. 2). They ate out the tender growing bud from the top of the coarse plant and the flower head with its great cluster of immature seeds. Most of the latter passed through the intestinal tract with little or no effect from the digestive juices, and were conspicuous in the droppings along the trails and streams.

By mid-August the fruits of mooseberry (*Viburnum edule*) (pl. 7, fig. 1) began to mature and soon the bears were eating them in quantities. They seemed to be very fond of these red, acid berries, most of which were almost unchanged by passage through the digestive tract. Apparently the berries had a laxative effect on the bears. The fruits are relatively short-lived, but for 10 days or 2 weeks in late August and early September they were prominent in the diet.

As is well known, the brown bear "caches" meat which is surplus to its immediate needs and returns when hungry to partake of it. I found only one instance of this habit, perhaps because at Katmai meat seemed to constitute a small percentage of the food. In this case the dead moose that we towed to the northwest shore of Grosvenor Lake to serve as bait for photographs (p. 159) was partially covered with gravel by the first bear to pass. The following night, presumably the same individual returned, jerked the carcass out of the gravel and ate a few mouthfuls despite an already bulging stomach. The bear's

attention was diverted for 5 to 10 minutes by scent or movement of a man concealed nearby. After the animal's nervousness was allayed, it did not re-cover the meat but went off and took a nap. Possibly it had forgotten its cache.

Fish as food and how they are captured.—Fish is an extremely important food. As described on page 162, the distribution of brown bears during June, July, and much of August is determined by the occurrence of migrating and spawning salmon. Despite their bulk, the bears are extremely quick and agile—as they must be to catch the fish in their aquatic environment.

Most fishing is done in riffles or other shallows where the water is less than 2 feet deep. Here the salmon can be seen, even in cloudy water, as they dart up the chutes or rest momentarily in eddies. On reaching the stream bank, the bear generally assesses the situation briefly, then walks into the water and endeavors to locate individual fish. On doing so, the animal rushes to the spot and tries to pin down the prey against the bottom with its front paws. In these charges, huge sprays of water are often thrown up, adding to the confusion and excitement. A series of unsuccessful attacks may end in the frustrated bear trotting to the shore, shaking its head and snarling with exasperation. It may try fishing in another part of the stream or may stand and look intently at the water in order to determine the channel in which the fish are moving. One bear that I watched on a river in northeastern Kukak Bay sat up on its haunches to get a better view.

When successful, the bear grabs and secures the fish between the jaws, walks to the shore, pins down the fish again with one or both fore feet, and proceeds to tear off mouthfuls of flesh and devour it. (Pl. 15, fig. 1.) Catching the fish with the paws and seizing it in the mouth are nearly simultaneous. However, in shallow water a better view of the action shows that the mouth-hold is definitely secondary. Occasionally the darting fish may be caught between the front paws as the bear is plunging with most of its weight on the hind-quarters, or it may be caught in the mouth. These latter catches, however, seem to be lucky accidents which result mainly from the salmon blundering into the bear in their wild rushes to escape.

Fishing success on shallow streams depends on many factors, including the agility, vigor, and experience or skill of the bear. It is easier to trap the fish in small creeks than in large rivers, although much larger runs in the latter may compensate to some degree for opportunities to corner the prey against banks in small creeks. Cer-

tainly the larger streams are patronized heavily by fishing bears, and shallowness of the water seems much more important than width. Another factor in successful fishing is vigor of the fish. In the early and middle stages of migration to the spawning beds, the salmon are alert, agile, and swift, and are extremely elusive. Later, as the fish become worn and weakened by their long struggle over rapids and shallows, they are less capable of escaping enemies, and the bears have easier "pickings." Spawmed-out salmon are exhausted and soon die if they are not set upon and devoured piecemeal or entirely. It is likely that late migrators are weak individuals and, with carrion, provide many opportunities for food late in the season.

Owing to numerous variables, it is impossible to provide an index of the rate of catch. I have seen bears at Brooks River in early July, 1953, make 5 to 15 attempts to pin down salmon before securing one. On the Savanoski River August 19, 1953, and at McNeil River August 26, 1954, bears caught salmon in five attempts or less. By late August, however, these fishermen appeared to have little appetite and exerted much less effort in running down their prey than bears that I watched early in the season.

Occasionally brown bears seek fish in water so deep that they cannot stand on the bottom. Under these circumstances the huge mammals are no match for the salmon in speed or agility. However, in deep pools at the foot of steep cascades or waterfalls, salmon may concentrate in such numbers that even the comparatively clumsy bears can snap up an unlucky or exhausted individual. We saw this type of fishing in operation at the cascade on McNeil River on August 26-27, 1954. At times several bears together or individuals swam and plunged about in the pool just below. The water was so deep that the animals' backs were almost or quite submerged at times. While I watched, a bear plunged about, darted its head below the surface and brought it out with a salmon clenched between the jaws. Brody told me that he also saw a bear, swimming in this same pool, clutch a salmon between its front paws as a man would catch a ball. The action was easily visible from the bluff south of the cascade, which was a formidable obstacle to migrating fish. Evidently the many salmon held up here temporarily attracted the attention of the bears.

Local observers at Katmai have stated that brownies, while swimming, catch salmon near the north bank of Savanoski River just above the delta in Iliuk Arm. The river in this area had cut a deep channel where any bear entering it would be forced to swim or float. While I saw a number of individual bears in the river at this point, I saw no

fish caught or actions indicating that the mammals were interested in food. It seemed improbable that salmon would concentrate here in the deep river, without barriers to their upstream passage, in numbers sufficient to attract bears.

Swimming.—The brown bear is an excellent swimmer, and on occasion individuals may go into the water purely for enjoyment. Despite its ability in the water and the procurement of much food in the form of fish, the bear is not as thoroughly at home in the aquatic environment as the moose. I have yet to see a bear take to the water to cross a large lake or a bay of Shelikof Strait, where a moose might well take the direct course in spite of icy water. In such a situation, the bear invariably prefers to plod along the shoreline.

Terrestrial obstacles are usually surmounted in preference to taking to the water, even when the latter course would mean a considerable saving of effort. On the north shore of Iliuk Arm and the south shore of Grosvenor Lake, long-used trails cut across the bases of short promontories. Bears that walked the sandy beaches chose to cross rough, stony ground or steep knolls rather than to wade, or swim short distances, around these promontories where wave action prevented sloping beaches from forming. Another instance may be observed on the northeastern shore of Lake Coville, where erosion had undercut the roots of alders, birch, and spruce so that for several hundred yards the fallen trees formed an impenetrable blockade of the beach. By wading in water less than 2 feet deep, the bears would have had a "water-level" route. Instead, their trail wound back through the woods, over a bluff nearly 200 feet in elevation, and back down to the beach beyond the fallen trees. I followed the tracks of a number of bears, all of which climbed the bluff rather than wet their feet.

On the other hand, I watched bears that seemed to enter the water with no apparent objective. One was seen late in July, 1953, floating quietly in a small, clear pond east of Hallo Bay. From our helicopter overhead it was evident that the animal was merely floating with all four legs spread wide. The day was sunny and unusually warm; presumably the bear was cooling off. On several occasions along the lower Savanoski River, bears were seen to enter the water, swim leisurely into the current and then drift downstream more or less sideways. After moving thus for varying distances up to 150 yards, the animals returned to shore, walked back to the point of beginning, and repeated the experience as much as four or five times. Two bears, apparently lone individuals, were seen performing thus at one time on

the afternoon of July 17, 1953. At times these animals approached within 50 yards but seemed to pay no attention to each other.

In every instance when the entire sequence was observed, the bears seemed reluctant at first to enter the water. Once wet, however, they evidently enjoyed it. None of the animals described above made any attempt to catch fish nor did any of them appear to look for fish in the very roily river water. I did not see any bear "dive" or go completely under the surface. In some instances the weather was cloudy, but at all times the air temperature was over 60° F. when the bears were swimming.

When swimming in water beyond its depth, the brown bear is completely submerged except for the head and the tip of the shoulder "hump." The head is held in a slightly elevated position so that the closed mouth is just above the water. I have been unable to observe the details of swimming in clear water in order to determine the movement of the legs, but presumably the front legs and feet are responsible for most of the forward motion.

Bear trails.—As I have pointed out, the brown bear is relatively sedentary during much of the summer when salmon furnish a dependable, ample supply of food. In spring, early summer, and fall, however, the animal may travel considerable distances. Individuals tend strongly to follow and to step in the footprints of bears that have preceded them. This leads to the establishment of deeply beaten paths with the individual footprints appearing as separate depressions. In the deep mat of tundra vegetation the footprints may be as deep as 5 or 6 inches below the level of the ground cover. Thus the major travel routes are clearly marked and often, in open country, are visible from afar. (Pl. 14, fig. 2.)

Most of these bear "highways" in the Katmai area ran parallel to the long axis of the major lakes such as Grosvenor, Coville, Naknek, and Brooks Lakes and Iliuk Arm. They followed the shores as closely as possible back of the high-water mark of severe storms, and often were on the dunes which had been built up by the storms (as on the north shore of Idavain Lake and northwest end of Grosvenor Lake). These trails cut straight across promontories, often climbing steep grades to cross the ridges. The brown bear usually proceeds between two points with the greatest possible directness, with the result in mountainous country that many of its trails are excessively steep. This was more striking on Kodiak Island than at Katmai, where the western tundra topography was comparatively gentle. Trails may be traveled extensively for many years, then fall into disuse. Such a

path was found east of Brooks Lake and has been described on page 165.

Brown bears may adopt a man-made trail or road and travel on it, sometimes while it is still used by people. The tractor road east of Brooks River which was utilized by Fish and Wildlife Service employees in hauling supplies and boats between Brooks Lake and Naknek Lake frequently bore the fresh tracks of bears. Most of the animals, however, seemed to avoid the road in favor of their own long-used paths in the vicinity. One of the most deeply worn of these bear trails was on a long-abandoned man-made road which led to a circular lake one-quarter mile southeast of the mouth of Brooks River. Bears also adopted the foot trail which was laid out by the National Geographic Society expedition of 1930 between the cabin headquarters on Iliuk Arm and upper Ukak River (whence the route led to the camp in the Valley of Ten Thousand Smokes). Because of travel by brown bears, this trail south to and around the northeastern slope of Mount Katolinat was easily followed and used by us in 1940, 10 years after it was abandoned by Dr. Griggs and his party. Although confirmation is lacking, I believe that long disused bear trails parallel to the south shore of Naknek Lake were originally the travel routes of native people moving across the Alaska Peninsula. Trails through Yori Pass, which run for several miles and are clearly evident from the air, may have originated through successive or joint use by primitive man and brown bears.

More haphazard wanderings in search of food may also leave traces, especially in summer. When a brown bear moves through dense grass, the latter is bent aside and smashed to the ground. If growth has largely ceased for the season, the grass remains prone and the trail is apparent for several weeks.

"Bear trees."—The Peninsula brown bear at Katmai uses "bear trees" but seldom in comparison with the grizzly and/or black bear of the Yellowstone Park region. In the latter area many conifers show the marks of repeated clawing and biting by passing bears. I saw only two instances of this practice at Katmai. One was in 1940, when a badly abused white spruce (*Picea glauca*) was found at the side of a bear trail near Brooks River. The second instance was in 1954, when we saw another "bear tree" on the spit that extended between the east end of Lake Coville and the backwater of Coville River. Bears frequently walked out on this wooded point en route to fishing in the rapids at the outlet of the lake, or to crossing the river. The trunks of these two trees, both white spruces, showed tooth- and claw-marks up

to a height of 6 feet, and bear hair was caught in crevices of the bark.

I can offer no explanation for the comparatively little use at Katmai of "trailside registers" (as they are surmised to be). Ample forest exists in which brown bears live and travel, so the opportunity for establishing record trees is present.

Rubbing pits.—As a sanitary measure and/or to relieve irritation, brown bears occasionally assume a sitting position and rotate on a fixed spot on the ground. In soft earth or sand a circular depression a foot or more deep is formed in a minute or two. I found such a rubbing place August 15, 1954, in the sandy beach on the south shore of the North Arm of Naknek Lake near the north base of Mount LaGorce. The depression was 3 feet in diameter and 2 feet deep in the center. Wet spots and footprints with water in them showed that the bear had been swimming or wading along the shore, and that my outboard motor probably had given the animal notice of my approach in time for it to withdraw only a few minutes previously.

In hard ground, rubbing pits are worn more gradually and probably are used at intervals over one or more seasons. They are essentially smooth, bowl-shaped depressions 2 to 3 feet in diameter and about 1 foot deep. Earth which is forced to the outside by the weight and lateral movements of the bear may form a low rim around the "crater," but this is beaten down and compacted so that the elevation is slight. Often several of these pits occur in an area of a hundred square yards. Perhaps they are made by a mother and cubs or by two or more adults, or quite possibly they are formed successively by one animal which returns to the spot repeatedly. Except on beaches, these rubbing pits endure for years because revegetation in the mineral soil is slow. I found most of the pits in wooded or shrubby areas; very few were on open grassland. In 1954 I found a set of three unused pits, one of which was several years old, on the point of a ridge a short distance east of Brooks Lake. The ridge was steep and rose above most of the trees that grew on the flats. Accordingly, the open area which had been frequented by the bear (or bears) afforded a fine view westward up the lake.

Resting.—Brown bears are prone to sleeping soon after making a meal, usually in the immediate vicinity. They lie down on any spot that is fairly smooth and level, and seem to prefer a grassy area. At Katmai, where the animals were not often disturbed, they frequently chose exposed or semi-open places. In localities where a large supply of food is available (such as a salmon stream or the resting place of a moose carcass) a bear may use the same bed a number of times.

Often, however, it sleeps on different spots in the same locality. The bed that has been used repeatedly can be distinguished only by the more thoroughly flattened and worn condition of the grass and other herbs. The size of the bed is not enlarged materially by re-use; this depends chiefly on the size of the animal. An example was observed early in July, 1953, when the carcass of a moose at the foot of rocky bluffs north of Brooks River furnished a supply of food for one or more bears. Two beds in the grass among scattered alders near the top of the bluff showed where successive meals were digested. The grass in these beds was permanently flattened and so crushed that the plants would not straighten again during that growing season.

In open country brown bears often lie down on ridge crests or other spots where extensive views can be obtained. Because of the animals' apparently poor eyesight, it may be more accurate to say that such places may command a wide range of scent-laden air currents. A bed in this type of surroundings was seen July 25, 1953, on the top of a hill which rose as an "island" in lower Katmai River. The south slope, which was covered with grass and clumps of alders, rose steeply to a long crest that dropped as a rock cliff back to near river level. The bed was on the highest point of the crest and overlooked the wide valley from Shelikof Strait to the crest of the Aleutian Range. Bear tracks and droppings were everywhere. It was apparent that the spot had been occupied repeatedly.

Ecological relationships.—Like all living organisms, the brown bear is only one unit in the cosmos of nature. It is dependent on many other species of animals and plants for food and concealment. Numerous species are affected by it, either beneficially or adversely. In the following discussion, an attempt will be made to point out some of these relationships.

The part played by salmon in the life of the brown bear has already been described in some detail (pp. 162-163 and 167-169). To summarize: Salmon flesh is the predominant item in the mammal's diet during June, July, and much of August. At Katmai, salmon constitutes the bulk of all flesh eaten throughout the bear's life. This abundant and easily procured food is the principal factor that determines the distribution of bears through the summer months. Areas that lack salmon streams are deserted by bears from June to August, whereas valleys with heavy runs of fish in the streams have a large bear population. As the runs decline toward the end of the season, the bears turn to other foods and scatter widely over the country.

Rainbow trout (*Salmo gairdneri*) are sufficiently abundant in some

localized waters to be a potentially significant item of food for bears that live in the vicinity. Trout, however, are more alert and even more agile than spawning salmon, particularly as the latter become progressively weaker in battling toward the headwaters of the streams. I have almost no information regarding the kill of rainbow trout by bears. Remains of this aquatic species were rarely seen on the stream banks, so apparently it is seldom captured.

The toll of salmon by bears and the effect on maintenance of the salmon population are subjects of much discussion in Alaska. Studies on Kodiak Island and elsewhere seem to show that brown bears, when abundant, kill large numbers of fish before the latter have deposited their eggs. It was not possible to make systematic observations of this habit in Katmai National Monument. Evidence of a general nature was common along numerous streams that bears killed considerable quantities of fish, many of which had not spawned. The bears were frequently "wasteful" and failed to consume all of each fish that was killed. Sometimes less than a quarter of the carcass was eaten, and occasionally a salmon was merely killed and dropped on the bank untouched except for the deep fang marks and a few claw scratches.

In management of Katmai Monument solely as a nature sanctuary, the problem of bear-salmon relationships may be limited to two questions: Are the fish sufficient to fill the mammals' need for food, and do the mammals keep the fish in balance with the aquatic environment? All signs indicate that the answers to both questions are in the affirmative.

The salmon run, however, is an important economic resource, and the Monument is one of the vital spawning grounds for the Bristol Bay fishing area. (Pl. 14, fig. 1.) The industry is prone to blame environmental factors for the decline of the resource. It is possible that the toll of fish exacted by the bears in the Monument will become a point of controversy. An effort should be made to obtain data that will clarify the role of these animals in the survival and production of salmon in the Monument.

Tracks and other signs show that brown bears and Alaska moose frequently use the same trails, but apparently they seldom meet. In the Yellowstone region the grizzly has been known to attack and badly maul or kill the Shiras moose, and it would not be surprising if a similar relationship obtains at Katmai between the two local species. However, no direct evidence of predation on moose was obtained. Several carcasses were found, but winter-kill (or possibly a fall in one

instance) was the probable cause of death. Moose carrion was fed upon by the brown bears even into midsummer when salmon were easily available. It was evident that the partially decayed meat was relished, for the bears that made the finds usually stayed nearby and made repeated meals on the carcasses. As a source of food generally, however, moose were not sufficiently abundant to be an important item in the diet. For this reason, it was not likely that moose calves were hunted systematically at Katmai. (The hidden young of more abundant ungulates such as elk are sometimes hunted by grizzlies.)

In the Katmai region rodents are hunted seasonally or when they come to the attention of foraging bears. During late spring and particularly in autumn, Arctic ground squirrels are sought in the grassland and on the tundra. Evidence of this pursuit was noted in a number of places. In late August, 1954, north of Idavain Lake at an elevation of 1,500 to 2,000 feet, I noted 5 spots during a walk of about 2 miles where bears had dug for squirrels. This digging probably had been done during the previous spring before the rodents had emerged from hibernation. From general observation it appeared to me that the bears at Katmai hunted ground squirrels considerably less than did their relatives at Mount McKinley National Park.

The Katmai bears occasionally tore into mouse runways, but wasted little effort in digging for such small game. In July 1954 I found a damaged beaver lodge on the north shore of Grosvenor Lake about 5 miles east of Coville River which may have been opened by a bear late the previous fall. A large food pile in the lake nearby had not been used and the many willow branches were sprouting vigorously. The evidence indicated that the occupants of the lodge had been killed or had left the area before the onset of winter.

On the larger salmon streams with open banks, brown bears usually were accompanied by flocks of glaucous-winged gulls. (See pl. 15, fig. 1.) Occasionally as many as 40 birds were seen hovering around one bear. On the whole the relationship was fairly peaceable with the birds walking about and pouncing on scraps or discarded carcasses of salmon the moment the bear turned away. The gulls, as well as other scavengers, benefited greatly from these discards of the bear's catches. At the same time the bear which was absorbed in fishing or feasting might receive warning of possible danger from its hangers-on, for the gulls were wary and never failed to maintain a lookout. Occasionally, however, the huge mammal became exasperated, owing perhaps to repeated failures to catch salmon, undue temerity of its avian companions, or other less obvious reasons, and lunged viciously at

the birds. Then an unwary gull sometimes was caught and killed, and the body devoured in a bite or two. Only the head, feet, wings, and much of the body skin with feathers attached remained as evidence of the bird's rashness or inexperience. In view of the number of birds crowded around the bears on the salmon streams, remarkably few fatalities resulted.

Magpies and ravens also took advantage of the remains of fish left by the feasting bears and sometimes accompanied the bears alone or with the gulls. In such cases the watchful and inquisitive birds may have aided in warning of approaching danger. Bald eagles might be found tearing at salmon remains while bears were fishing or eating nearby. Being comparatively clumsy on the ground and slow to get into the air, these big scavengers were careful to maintain a distance of at least 100 feet. All four of these carnivorous bird species took advantage of the bears' leavings, often days after the mammals had left the scene.

Relations with man.—Undoubtedly the brown bear was one of the most important wild land mammals in the daily life of the earliest men in the Katmai region. Toward people armed only with primitive weapons, the bear may have been much more aggressive than it is today. Nevertheless, although it has become somewhat acquainted with firearms and may be more prone to flee from modern man, the animal is still a factor in public use of the Monument. Because the brown bear is so powerful and reputedly dangerous, I will close this discussion of the species by summarizing and commenting on the available information concerning bear-man problems.

The Eskimo hunted and utilized the brown bear. Davis (1954) found bone material belonging to this species in his digs of 1953 at Kukak and Savanoski. The following year Oswalt reported finding the bones of brown bear in excavating the Kafia Bay site. He did not furnish details, and no traces of bear were included in the material which was reexamined later by C. O. Handley, Jr. Whether the bones were refuse from food material or had some other significance is not known. (Oswalt, 1955, p. 34.)

A method of transporting bear meat which was once used by the local natives was described to me in September 1940 by one of several Eskimo from "new" Savanoski on the Naknek River. They had come to Brooks River to seine for salmon. Seeing me examining a crude frame for a one-man boat (pl. 13, fig. 1) which was lying among the willows near the outlet of Brooks River, the man explained its past use. According to him, a hunter would walk up the Savanoski River

until he succeeded in shooting a bear. He would then make a boat frame from alders that he would cut nearby. The bear would then be skinned and the hide used to cover the frame, the hair being inside. Cutting up the carcass, the hunter would load the meat in the boat and, guiding himself with a pole, float down the river to Iliuk Arm. There, or at Brooks River, he would be met by his family or friends in a motor-driven boat which, because of its draft, would not be usable in the swift, shallow Savanoski River. My informant added quickly, "This was before the Monument was extended and took in the Savanoski River valley!"

The boat frame, which had been discarded at least a year before I saw it, was about 7 feet long and $3\frac{1}{2}$ feet wide amidships. The ribs and other members had been lashed together with light-colored cotton or linen cord like that used in salmon seines. I did not obtain the name of the Eskimo who gave me the foregoing information. He was a small man, probably between 40 and 50 years of age, whose right hand was injured or crippled and covered with a black leather glove.

In a sanctuary such as Katmai National Monument, the brown bear comes into direct contact with man chiefly in three types of localities: (1) on salmon streams; (2) on trails; and (3) at camps. (As hunting is not permitted in the Monument, relatively few contacts are made outside of these three types of places.)

Abundant evidence was found that bears used man's trails in the Katmai area. Old travel routes, probably made by native people, sometimes were kept open and traceable long after use by humans had ceased. Examples of these were trails along the south shores of Iliuk Arm and Naknek Lake, and that across the lowest pass between Kuliak and Kukak Bays. Much of the trail west of Ukak River which was made by the National Geographic Society expedition in 1930 and then abandoned was still in excellent condition 10 years later as the result of travel by bears and moose. Considerable use by the former species was evident in 1953 on the portage between the Bay of Islands and Grosvenor Lake. The trail was used only infrequently by people but fairly constantly by the bears. The same was true of trails and abandoned roads through the spruce forest east of Brooks River.

Even areas which were currently utilized by persons and machinery were not avoided. The rough tractor road between the outlet of Brooks River and the Fish and Wildlife Service salmon research laboratory was used several times weekly during July and August, 1953 and 1954, and a small tractor was driven over it at least once a week from early May to the end of August. Yet bear tracks were often

seen on the road. On August 23, 1954, I noted fresh tracks of a small brownie in the dirt which had been thrown up by the tractor only two days previously.

A few raids on camps have been made by brown bears in Katmai National Monument. I learned of only two such incidents, up to the fall of 1954, that have occurred when a person was actually in residence.

A brief account of one of these cases was given to me by Roy Fure, who has lived in a cabin on the north shore of the Bay of Islands since 1916. The incident took place many years before it was described to me in July 1953. During the owner's absence for a few days, a bear made several attempts to break into a food cache about 30 feet behind the cabin. The storehouse was strongly built, however, and the animal did not gain entrance. Seeing the damage on his return, Fure was alert and prepared when the bear returned and this time directed its efforts to the main cabin. Hearing the occupant's shouts, it retreated about a dozen yards, whereupon Fure opened the door and shot it.

The second incident occurred around the end of the first week in July, 1953. It was described to me on July 29 by Otis Martin of Houston, Tex., a salmon-stream guard employed for the season by the Fish and Wildlife Service. He was asleep about 2 a.m. in a small tent 1 mile south of Kaguyak Village site, on the shore of Shelikof Strait. The tent was barely large enough for the bunk, a tiny table, a gasoline stove and stock of food, with a narrow aisle alongside the bed. Awakened by snuffling sounds and scratching at the canvas, Martin shouted and picked up his loaded rifle which was on the floor. A moment later claws tore a gash in the tent wall and the head of a large bear was thrust through the opening. The man hastily fired at the forehead, which was hardly more than a rifle length away, and the animal dropped in its tracks. The huge body fell against the door, which was on a wooden frame, and completely blocked the exit. The stream guard was unable to move the carcass or even roll it away from the doorway, and was forced to use the slashed opening in the wall until help arrived. The combined efforts of four men were required to roll and pull the body down the sloping sand beach to get it away from the tent.

In each of these incidents the bear attempted to force its way into a camp which was occupied by a person. It seems possible that only an armed defense by the occupants prevented the bear from inflicting serious injuries or worse.

Brief mention should be made of less aggressive behavior—or

rather lack of fear—on the part of brown bears toward man and his possessions at Katmai. In mid-July, 1953, one or more animals walked within 50 feet of our Savanoski camp during a 2-day interval when it was unoccupied. A bear also walked across the mound of soft earth which had been excavated two or three weeks previously by the Project archeologists. About August 11, 1953, George Peters saw a bear eating from a garbage pail about 50 feet from the Park Service ranger station (a tent) near the outlet of Brooks River. Shouts induced the animal to leave, but only slowly and without any sign of timidity. The display of boldness caused Peters to adopt the practice for the remainder of the season of taking all garbage twice daily to a distance of about half a mile. At the end of our 1953 field season I occupied the ranger station alone. On the morning of September 15 I found that during the previous night a bear had clawed and torn a life jacket that had been left on the ground about 10 feet from the tent where I was sleeping.

Wendell Oswald told me of two experiences with bears in Kafia Bay during his archeological work in 1954. One evening about July 1 he made two trips for water to a small stream a few hundred feet from his camp. On going for the second pail of water, he found the tracks of an adult bear and cub which had followed his earlier footprints for some distance. Asleep in the same camp early on July 11, Oswald was awakened by a mother bear and yearling cub snuffing vigorously at the canvas near his head. When loud shouting did not rout the animals, he beat two cooking pans together. The bears then ran to a knoll about 40 yards away, where the adult stood on her hind legs to stare at the man as he emerged from the tent. The bears then left.

In none of these cases did the animals become aggressive. They merely showed indifference or curiosity at the presence of man or strong scent from his recent presence. Possibly this bold attitude resulted in part from absence of hunting or other disturbance which outside of the Monument may engender fear or caution in the animals. It becomes important only if it leads to attacks and mauling.

A few raids were made by bears on camps or caches which had had no recent use by man. One of these was made during the 1952 field season on a "spur" camp which had been set up by an Army Engineers' survey party on the south shore of Iliuk Arm. The site chosen was alongside the largest creek which descended the north slope of Mount Katolinat. This stream was a spawning area for rather large numbers of salmon and during the summer was frequented by bears. Under

these circumstances camp supplies were almost certain to be raided, particularly if left unguarded for several days as these were.

Our camp on the south shore of Naknek Lake about 1 mile north of Brooks River was invaded by a bear late in July, 1953. Cans of food which had been stacked outside were chewed open. Even a case of motor oil in quart cans was ripped open and the contents were drained. Doubtless the animal was attracted to the site by the remains of garbage which had been incompletely burned and by the carcasses of birds and small mammals at a laboratory work table. The tent, which was closed, was not molested, probably because it had not been used for cooking or storage of food. This camp had not been occupied for at least a week prior to the bear's visit.

Early in the spring of 1954 the kitchen and mess hall of the public camp at the mouth of Coville River was wrecked by a brown bear which did an estimated 300 dollars' worth of damage. The building, which was of flimsy, prefabricated construction, was easily torn open for entry and the food supplies were similarly accessible. The animal devoured practically every kitchen item it encountered, including soap bars and flakes, lime, and paper towels and napkins. The impact of such material as lime and soap on the animal's digestive system caused a quick and violent reaction. In rage or pain, the bear smashed tables and benches in the mess hall and mauled a cottonwood tree a short distance outside, tearing off most of the bark and biting into the wood of the lower trunk.

Our campsite on Coville River, about 300 yards west of the public camp, was entered by a young brown bear on the morning of July 25, 1954, while it was occupied by Schaller and me. I was aroused by the sound of an animal moving around our outdoor table about 15 feet from our sleeping tent. Looking out, I saw a yearling bear lying on the ground nosing at something which it was holding between its forepaws. Noticing my head appear, the animal jumped to its feet and rushed off in great fright. This bear, which was inexperienced and timid, had almost certainly been attracted by some decaying fish which Schaller was "ripening" in a waterproof sack for bait to bring bears within camera range. Although he had intended to use the bait at a distance from camp, the efficacy of the material was demonstrated fully.

Two caches of the Katmai Project which were established in the fall of 1953 were found by brown bears before mid-June of the following year. Thirty-two cases of standard Army rations were piled by Robert Luntley on the grassy ridge back of our campsite at Savanoski, covered

with a tarpaulin and roped securely. These tinned rations were sealed in heavy weatherproof fiber containers, and the canvas and rope were not contaminated by food odors. Apparently, therefore, the animal or animals dug into the cache primarily to satisfy a sense of curiosity, and an experimental bite revealed the presence of food. Signs indicated that the cache was opened and all food devoured between its establishment during the first week of October and the beginning of the hibernation period.

A second cache consisting of a dismantled folding boat was placed on a little island in Grosvenor Lake during the summer of 1953. The island was about 50 feet from the south shore of the lake and near the north end of the portage trail to the Bay of Islands. The canvas boat consisted of a solid package about 5 by 2 by 2 feet in size, just as it was received from the manufacturer. It had never been opened and therefore was not contaminated by food odors. The waterproofing material appeared to be of mineral tar origin. In the absence of suitable trees and because of its weight the package was left on the ground for possible use in the 1954 season. Sometime between early October, 1953, and mid-June, 1954, the bundle was pulled about and probably turned over by a bear. A long tear and numerous claw-punctures rendered the boat quite unfit for use. The relatively small damage to the canvas indicated that the bear had not been enraged, for in that case the fabric would have been ripped to shreds and scattered about. Curiosity appears to be a plausible explanation for the animal's actions in this instance.

Absence of food or food odors thus may not guarantee immunity for man's property from the attentions of brown bears. Curiosity or inquisitiveness seems to have been a strong motivating factor in the actions of several of the animals which have been mentioned above. Therefore it is not advisable for persons to depend too strongly on fear of humans or human scent to keep bears at a distance. For example, a man who is completely immobile—as in a sound sleep—may be approached out of curiosity and then injured when the animal is suddenly startled at close quarters.

In any evaluation of so-called "marauding" propensities of brown bears, human failures and omissions should be considered. Practicable measures can be taken at established camps which will greatly reduce their attractiveness to bears, with corresponding increase of safety for persons and food or other property. These measures, which include the erection of food caches and disposal of garbage and discarded food containers, are well known in the Alaskan wilderness and need no description here. They are, however, often disregarded.

Temporary camps, naturally, have been safeguarded least. Their occupants generally have assumed that precautions could be minimized and the camps abandoned before being found and raided by the animals. As noted, this assumption has not always been justified. Even worse, the occupants of well-established, practically permanent camps have been seriously negligent.

At the Brooks River public camp care was taken to safeguard food supplies and to remove wastes from the occupied area. Bears or their sign were commonplace in the vicinity but as a rule they avoided the camp which was occupied continuously through the tourist season by 3 to 30 persons. In September 1954, however, food was deliberately exposed for several nights in an "experiment" to determine if brown bears were sufficiently bold to enter the camp while it was manned. A medium-size bear took and carried off the bait, but apparently no immediate damage resulted. Thoughtlessness, however, can lead to serious difficulties, hazard to human life, and demands for destruction of the bears.

Over-eager photographers can get into trouble and establish another type of problem for the area administrators and, indirectly, for other members of the visiting public. In July 1954 bears were baited to a refuse dump by depositing there salmon which were found dead or badly injured at the counting weir across Brooks River. Photographs were made at night with the use of flash by persons *on the ground*. It was said that several pictures were made with hand-held cameras as close as 15 feet from the animals. This behavior by amateurs who were unacquainted with bear psychology and habits was risky in the extreme. It could also cause a delayed type of hazard by irritating the bears which might later attack fishermen or other unwary visitors in the heavily used area along Brooks River. (Pl. 13, fig. 2.)

In contrast with the aggressive behavior of a few bears that has been described on pages 178 et seq., several demonstrations of timidity can be cited. While climbing a grassy ridge on the north side of Mount Katolinat in September 1940, I came suddenly on two adult females with two yearling young. Even at 75 feet the bears required several minutes of gazing to find and identify me. Then they raced off in a great fright and were still galloping when they disappeared from view about a mile away.

Early in July, 1953, the helicopter mechanic of the Katmai Project, Donald Sanders, attempted to ascend the lower Savanoski River in a skiff. Before he reached camp, the skiff went hard aground on a shoal. Being unable to get free, Sanders decided to wait for dawn

and went to sleep in the boat. A number of times he was awakened by bears splashing, either fishing for salmon or swimming. Each time he stood up and shouted, whereupon the animals left. He estimated that several of them had approached within 100 feet—although in the darkness they seemed *much* closer!

The sound of an outboard motor was enough to cause a brown bear to flee as we approached the head of Devil's Cove (north arm of Kukak Bay) on August 5, 1953. The animal, which was walking east on the north shore, heard the sound at a distance estimated at 1,000 feet. After standing until we were about 500 feet off, the bear turned away, broke into a trot, and disappeared up an alder-covered ravine.

Several demonstrations of timidity were observed during our field work in 1954. During the night of July 6-7 a medium-size bear walked east along the north shore of Lake Coville. Less than 100 yards from Coville River (which, with its spawning salmon, probably was the objective) the animal came to a point 20 feet from our tents. Track marks visible the next morning showed that it then turned and walked back in its own trail. After some distance the traces were lost when the bear turned off into the woods. Two nights later a bear (not necessarily the same) which Schaller had hoped to photograph at a moose carcass rushed off in the darkness when the man noisily descended from his concealment in a spruce tree. (See p. 159.) A similar reaction of fear toward man was manifested by the bear that I startled in our Coville camp on July 25, 1954. (See p. 180.) This animal appeared to be a yearling cub which might have been much more easily dismayed than an adult.

Some of the bears seen at McNeil River on August 26, 1954, also showed fear of man in greater or less degree. A large animal that approached over a ridge only 75 feet away either saw or scented me and vanished silently in the alders. In two other places along McNeil River three bears that detected my presence abruptly left their fishing and dashed away in evident fright. It should be noted that this area was open to hunting and the animals may have gained experience with man as a deadly enemy.

One of the bears at McNeil River proved to be unusually docile. Soon after daylight on August 27, 1954, we saw a medium-size to small bear slowly making its way west along the south shore of the lagoon at the mouth of the river. It appeared to be looking for food on the beach which was exposed by the low tide. The bear obviously intended to climb the bluff at the foot of which our airplane was beached, while we waited for the tide to refloat it. Although clearly fearful of

the strange object and our presence, the bear passed only 75 feet away in order to reach a low place in the otherwise sheer bluff. Schaller decided to get photographs and found that the animal was unexpectedly tolerant and unresentful of being followed. For the next hour the man trailed his subject at distances that ranged from 100 to as little as 30 feet, with no evidence of bad temper or timidity. During much of the time the bear looked for salmon in the river, but showed no resentment when the photographer pressed in close for shots. This animal appeared to be in its third year and obviously had had no unpleasant experience with mankind.

At this point in our discussion of the species' relations with man, the reactions of the brown bear to aircraft should be described briefly. Little or no attention seemed to be paid to airplanes when the latter were at altitudes of 2,000 feet or higher, or at distances exceeding three-quarters of a mile. At closer quarters, however, most animals that I observed showed reactions that ranged from uneasiness to great fear. An adult brownie on a mud flat in the lower Savanoski River on July 2, 1953, seemed badly frightened by our plane as it circled overhead at 1,000 feet altitude. In the same area on July 17 a plane flew down the valley at an elevation that I estimated from the ground at 500 feet. A bear that had been swimming in apparent playfulness (pp. 169-170) lunged and looked upward at the sound of the motor, then turned and swam for the nearest wooded shore. As soon as the animal's feet touched bottom it rushed up the bank and into cover in a flash.

In most cases the reaction to helicopters was similar. Ten bears were scattered about over the wide mud flats along the spreading river-channels back of Hallo Bay when we sighted them about 7 o'clock in the evening of July 24, 1953. On a course from Kaguyak to Kukak Bay, we were moving about 75 miles an hour at an altitude of 300 to 400 feet. When the 'copter was nearly half a mile off, the bears became agitated and within five or six seconds all were running at top speed for the nearest cover.

On another occasion (August 19) some bears showed less fear. As we settled for a landing on the gravel shore of the Savanoski River about 1 mile west of Rainbow River, 5 bears were fishing for salmon or walking about. Four of the animals, which were within a hundred yards of the woods, ran into cover. The remaining bear was far out in the open at the edge of the main stream channel and, although it looked about uneasily several times, did not leave. Possibly the roar of the water partially masked the sound of our rotor blades. Later,

when we flew on down the Savanoski River to the mouth, we counted 23 bears in the water and on the bars. One of these animals fled in panic when the 'copter was still more than half a mile off, and it continued galloping nearly that distance until it was near woods and we had passed far by. Most of the other bears, however, paid little attention to the helicopter, provided it was more than 500 feet away in horizontal distance and at a similar height above the ground. Again, the noise of the river, which was extremely swift and turbulent, may have partially muffled the 'copter's throbbing roar.

In summarizing the reactions of brown bears at Katmai to aircraft, it was evident that the sound of motors was greatly feared by the majority of the animals observed. An airplane obviously was something to be avoided. It is possible that some shooting from the air has occurred despite Territorial game laws and the legal status of the National Monument. It is more likely that "hazing" of bears by circling and diving at them has taken place, for this hazardous pastime is not rare in Alaska. For the protection of the wildlife, maintenance of normal habits, and promotion of easy viewing of bears by the visiting public this problem should receive attention by the National Park Service.

A weighty obligation rests on the Park Service because of the presence of these huge creatures. It is not enough to preserve any given number of bears in the Monument. They must be allowed to pursue their normal mode of existence, as far as possible, despite use of the area by visitors. Means for insuring the latter's safety must avoid disruption of the bear population, for these animals constitute a major asset and attraction. Another protection problem arises from the rapid encroachment of civilization in the surrounding region. Economic demands are pressing on this formerly remote area and the pressure will increase as natural resources elsewhere are used up. Among these resources in the Monument is the salmon, which is a major item in bear diet. The Park Service must be prepared to resist attempts to reduce this drain on the fishery in order to increase the commercial catch. Certainly, the American public can afford to maintain these largest representatives of the world's greatest land carnivore—the Alaska brown bear—throughout the foreseeable future.

Mustela crminea arctica (Merriam), Short-tailed Weasel or Ermine
M. rixosa eskimo (Stone), Least Weasel

The weasels are among several mammals the presence of which can be detected readily in winter but which are seldom found during the

warmer months. No information concerning distribution and abundance of the weasels was obtained in the period of the Katmai Project. *M. c. arctica* has been taken in nearby areas, at Becharof Lake and on Ugashik River. There is one specimen of the least weasel in the U. S. National Museum from "vicinity of Bristol Bay."

I saw a small weasel at the salmon cannery in Kukak Bay on October 7, 1940. As I was crawling cautiously over the partially burned dock to reach land, the animal emerged from the shrubbery on shore and ran about on the open timbers. It showed no fear but rather a lively curiosity, and after a few minutes it disappeared. It was probably a least weasel.

Mustela vison (subsp.?), Mink

The only mink we saw was captured July 30, 1953, in a steel trap in the repair shop of the abandoned cannery at Kukak Bay. A large number of meadow mice had been confined there for several days previously by Schiller, who was catching the rodents alive for use in pathological studies. The mice were kept in a steel-lined locker without a lid. In less than 24 hours 35 of the captive animals were killed in a manner indicating that a mustelid was the predator. Several No. 0 traps were set around the cage, and the mink was caught.

This animal was a small adult female which we managed to confine, virtually unharmed, in a rough cage. Within an hour or two the mink killed and ate a mouse which was provided, as well as a portion of the head of a salmon. The following morning it ate two mice and some more fish. However, late that afternoon the mink became unconscious and died an hour later. An autopsy revealed an intestinal obstruction and numerous perforations of the intestines due to fish bones.

A few signs of mink were found on beaver dams and along lake shores in the western portion of the Monument. Apparently it is not abundant in the area.

Gulo luscus luscus (Linnaeus), Wolverine

This is a widely distributed species as well as the most far-ranging of the smaller mammals. Wolverines have been found in the Monument from sea level to 3,000 feet and it is likely that they ascend higher on occasion. While nowhere populous, the species in this area appeared to be comparatively numerous. We noticed tracks on the shore of Iliuk Arm in 1953 and 1954 and on the south shore of Grosvenor Lake in the latter year.

We have several sight records of this rather elusive animal. I

watched one, October 5, 1940, as it loped along the beach of Hidden Harbor in pursuit of a group of mallards. The approach of our gasoline-powered boat alarmed the ducks, whereupon the wolverine snarled at us, turned and disappeared in the alders.

William F. Thompson, Jr., reported seeing a wolverine northwest of the head of Kukak Bay, at an elevation of 2,500 feet or more, on July 25, 1953. The animal was loping or galloping down the mountain-side.

Another wolverine was found in an extraordinarily barren environment on Mount Ikagluik, east of the lower Ukak River. On August 17, 1953, Werner Juhle requested our helicopter pilot, Donald Williams, to fly him to the great craterlike depression in the upper portion of that mountain in order to determine whether it was volcanic in origin. Because of the hazards of swirling air currents at that elevation, and the need for lightening the aircraft, I did not join in the trip. When the 'copter landed on the floor at the rear of the "crater" at an altitude slightly over 2,900 feet above sea level, a wolverine ran away up the rocky wall. On this slope, which by Williams' estimate was 70 to 80 degrees, the animal ran without apparent effort. It disappeared into a hole that had the appearance of a den rather than a chance opening in broken rock of the talus slope. The entire "crater" (which was probably formed by erosion rather than volcanism) was barren of vegetation. Williams said he saw no evidence of the presence of other animals, such as ground squirrels.

In mid-July, 1954, a wolverine was seen in the lower valley of Margot Creek, south of Iliuk Arm, by Richard Ward and John Greenbank. Possibly the same animal was encountered on the evening of July 23 by Garniss Curtis on the beach at the outlet of Margot Creek. In the latter incident the wolverine did not show signs of alarm. It loped away but paused every 50 to 75 feet to look back at the man. It did not take shelter in the brush until it was several hundred yards away.

Davis (1954, p. 19) recovered bones of wolverine from his excavation of a prehistoric Eskimo site at Kukak in 1953.

The wolverine and the wolf are symbolic of the northern wilderness. Katmai National Monument serves an important purpose in conserving them for future generations.

Lutra canadensis yukonensis Goldman, River Otter

This interesting and graceful species was numerous on the lakes and larger streams of the Bering Sea slope. It also inhabited the bays

and lower stream courses on the coast of Shelikof Strait, but apparently was less abundant there.

Because it enters these coastal waters, the river otter may occur in the same habitat as the sea otter. (See next account.) The two species might be confused by the uninitiated observer who saw an animal swimming at a distance. The sea otter, however, is likely to have much more white on the head and neck. The chin and upper throat of the river otter are grayish-white, but this color rarely or never extends to the upper parts of the head and neck. Both species are easily distinguished from any seal by the small front feet (instead of large flippers) and the large conical tail.

Sand spits, beaches, and mud flats on the shores of the larger lakes in the western portion of the Monument are the most likely places to find the sign of the river otter. These places, and similar spots on the river banks, are frequented by this playful and sociable animal. Numerous tracks may be found there, as well as the droppings, which are composed largely of the fragments of aquatic invertebrates such as fresh-water mussels (*Anodonta beringiana* Middendorf) and snails, and the scales of fish.

Otter sign was recorded at the following localities in 1953: West shore of Brooks Lake near the outlet of Headwaters Creek, June 30; west shore of Iliuk Arm about one-half mile southwest of the Narrows, July 1; on Big River 5 to 7 miles northwest of Shelikof Strait, July 24; near an unnamed lake west of the portage between the Bay of Islands and Grosvenor Lake, September 1; a small clear-water tributary of Douglas River about 6 miles above the outlet of the latter, September 3; and on the north shore of the North Arm of Naknek Lake north of the western entrance to the Arm from Naknek Lake proper, September 7. The following year, many tracks were noted at the outlet of a creek on the north shore of Grosvenor Lake about 3 miles east of Coville River. I saw signs of the animals at numerous other points without making records of the various occurrences.

Otters were watched on two occasions near the close of the 1953 season. On September 9, as I was standing on the southeastern shore of Brooks Lake at the outlet of a small creek, I saw two otters swim past about 200 feet away. From the considerable difference in size I inferred that the animals were a female and her young. The latter gamboled about the mother which then reared and tumbled in the water. At one point, for about 10 seconds, the youngster appeared to ride on the mother's back. The pair dove repeatedly except during these interludes of play. Swimming on the surface for only a few

seconds, they would disappear for 10 to 20 seconds (by rough count). They stared fixedly at me once as I stood in the open near the water's edge, but otherwise paid no evident attention. On coming up from a dive, the adult otter held a fish about 9 inches long crosswise in her mouth. Using eight-power binoculars, I inferred from the shape and yellowish coloration that the prey was a Dolly Varden trout (*Salvelinus malma malma* Walbaum). The two animals continued on southwest, parallel to the shore, and disappeared in the distance.

A few days later, on September 12, 1953, I found an adult otter, presumably a female, with three half-grown young. As I looked down from the top of a 15-foot bluff on the largest island in northwestern Iliuk Arm, about 2 miles east of the Narrows, a movement on the lower level of the island attracted my attention. Careful examination showed four otters together in the rank grass. They were literally in a heap, with the young crawling over the mother and each other. I failed to determine whether the latter were nursing or attempting to do so. In a few minutes the otters moved slowly through the grass to open rocks near the water. Two or three times the mother stopped to scratch her neck and ears with a hind foot, dog fashion, and every time each of the young followed suit immediately. This almost instantaneous mimicry was amusing and interesting as a manifestation of the learning process.

The animals soon entered the water and swam around the north side of the island to the east margin where I had come ashore. (Pl. 15, fig. 2.) As they perceived my scent, which was carried out over the lake by a west wind, the mother gave loud alarm signals. Her repeated snorts sounded much like a man clearing his throat violently while keeping his mouth open. She became visibly more agitated at seeing my skiff which was tied up among the boulders. Snorting faster, she appeared to scrutinize the slope of the island for the source of the danger. Almost immediately she saw my head as I watched from between the rocks on the skyline. Turning, she swam as fast as possible for the north shore of the lake one-quarter mile away. The three young followed closely, swimming well and in the typically undulating fashion.

The island where this episode occurred was occupied by a small nesting colony of glaucous-winged gulls. At least two young gulls, still in their downy plumage, were on the island and did not enter the water when I went up to them. A few juvenile double-crested cormorants, still unable to fly, swam away as I approached. If the otters were foraging, they may have been looking for tender food in the form of young birds.

Men of the U. S. Army Engineers who were engaged in topographic survey work in Kukak Bay during the summer of 1953 told me of finding two animals, which apparently were otters, on a small island in the upper bay. As described to me, the animals were seen early in July. They were "reddish-brown" in color, had sizable tails, and moved in an undulating lope. They were much larger than either mink or marten, and definitely were not foxes. The island, which was small and almost barren of vegetation except grass, was the nesting site of some short-billed gulls. The surveyors attempted to kill the animals and destroyed a number of gull eggs in the chase, but were unsuccessful. When I visited the island about a month later, the colony appeared to have had poor nesting success. As to whether this was due to predation, to disturbance, or to other factors, no conclusion could be drawn.

The river otter is a valuable furbearer which will require some vigilance to protect from poaching. At the time of our study the population within the Monument appeared to be in satisfactory condition.

Vulpes fulva kenaiensis Merriam, Red Fox

The most abundant carnivore in the Katmai region is the red fox. It is widespread below the 750-foot contour, and apparently it occurs in most ecological environments down to sea level. I found fox tracks or other signs within the Monument on coastal beaches, lake and stream margins, grass-alder valley bottoms, open grasslands, margins of mixed forest, and willow swamp. Scattered evidence indicated that the species was also numerous west of the Monument as far as the shore of Bristol Bay.

Signs of foxes were noted in so many localities that a complete list would have little significance. The animals seemed most abundant in the lower valleys behind Katmai, Dakavak and Kukak Bays, on Kuikpalik Island (a long-abandoned fur "ranch"), on the north shores of Lake Coville and Grosvenor Lake, and around Iliuk Arm. No sign was found higher than 750 feet elevation, but it is probable that the species occurs a little higher.

No difference in abundance was appreciable between the seasons of 1953 and 1954. It appeared to me that foxes were somewhat less numerous during those years than on the occasion of my first visit to Katmai in the fall of 1940. This is only an impression, however, and is not based on statistical evidence. Some trapping pressure was being exerted by poachers at the time of my first stay in the Monu-

ment, and the red fox population should have shown evidence of depletion. The effect of trapping probably was limited to three or four localities: Brooks River, lower Savanoski River, Amalik Bay-Geographic Harbor, and perhaps the west end of Brooks Lake.

During the 1920's Kuikpalik Island in Shelikof Strait was utilized as a fox "farm." Although the island was far enough from the mainland to prevent the furbearers from escaping by swimming, an enclosure about 100 by 150 feet was erected to confine at least a portion of the stock. The posts of this enclosure were still standing at the time of my visit on July 29, 1953. Two residences (including a two-room cabin) and three small structures for feed, pelt storage, etc., were in poor condition. Periodicals in the larger residence indicated that it was last occupied in 1929. The house was open and the presence of fox droppings showed that it had been a favorite resort of the animals. One dropping was made up largely of fine white fur—presumably snowshoe hare.

Soon after Messrs. Davis and Leach began excavating a prehistoric camp site near Kukak Point on the north shore of Kukak Bay in July 1953, they became aware of a fox den in the grass-covered dunes only 50 feet away. Not being molested, the two parent foxes quickly ignored the disturbance. In a few days they were coming to the dig for handouts of scraps from the archeologists' lunches.

In the company of Messrs. Davis, Leach, and Schiller, I spent several hours on August 2, 1953, observing these foxes and their family of six half-grown young. The following observations of behavior were made.

The adult male was much the boldest member of the group. Although he had never encountered Schiller or me, he readily took food from our hands within a few minutes. He reached for the offerings with deliberation, grasped them between the incisor teeth, and was careful to avoid touching our fingers. Most bits of chocolate were eaten at once; other items such as bacon were carried away, presumably to be buried or hidden in the den.

The mother (pl. 16, fig. 1) was much more restless or nervous than her mate and considerably more cautious. She seldom came closer to us than 12 feet; however, she had sometimes approached more closely to the two men to whom she was accustomed. She picked up food that was thrown to her. Unlike the male, she ate very few tidbits on the spot but carried them off for caching.

The pups were much more wary of us than either of the parents,

never approaching closer than 25 feet. When neither parent was present, the pups remained in sight only briefly before running back into the dense grass behind the beach. On the open sand they ran awkwardly and undoubtedly could have been overtaken by an agile man. All the pups were in splendid condition, but the mother was noticeably thin and her coat was somewhat ragged.

On our arrival at the den (about noon), the male parent was on a small island in the bay about a quarter of a mile offshore. I was informed that he had gone to the island earlier in the day at low tide when the swimming distance was only a few yards. Our presence near the den—or perhaps the possibility of food offerings—noticeably excited the male. For about two hours he alternately trotted back and forth along the water's edge, or sat gazing fixedly in our direction. It was obvious that he disliked to undertake the long swim in the icy water.

Finally the fox waded in and started paddling in our direction. This action coincided with the entrapment of a female pup in one of several small traps which Schiller had set in order to obtain two live animals for study. It is likely that the male parent observed the excited reaction of the mother, and this overcame his reluctance to enter the water. He swam steadily with about an inch of his entire length from nose to tail-tip showing above the surface. As the tide was ebbing, he was carried on an approximate 45-degree diagonal and landed about 300 yards away from us. Immediately he ran up the slope to an area of dry, loose sand where he rolled and pushed himself about to dry his wet fur. After a minute or two of tumbling the fox started trotting toward us. His course took him past our helicopter which was sitting inert on the sand; he stopped twice to stare at it as he went around it about 20 feet distant. Perhaps the sight of the strange object as well as the 15 or 20 minutes required to swim the channel caused the male fox to forget the original alarm of his mate. At any rate, he came walking up to us and accepted food immediately. His fur was only partially dry and at intervals he shivered violently with cold.

After obtaining several bits of bacon and chocolate, the male fox went over the grassy dune in the direction of the den. He returned in company of a pup, with which he played briefly. Later he went off into the grass and was gone 10 minutes or more. As he reappeared, his mate raced to him whining and squealing, reaching her muzzle up to his and jumping about. I assumed that she was begging for food which she had expected him to bring back from the grass-covered dunes.

Schiller (Schiller and Rausch, 1956, p. 194) found that the two young foxes mentioned above, which he captured at Kukak Bay in 1953, harbored hookworms (*Uncinaria stenocephala*, Railliet, 1884) and tapeworms (*Taenia* sp.).

Rabies has been identified in red foxes in the region of the Monument. Rausch (1958) reported the killing of a rabid fox at Naknek on April 25, 1954. During the previous month several red foxes were destroyed at Kanatak, only 25 miles from the southwest corner of the Monument, when they attacked the natives' dogs. Other foxes were found dead near Kanatak after the snow melted, but tissue was not saved for examination. Rabies has not been diagnosed in any animal within the National Monument, but cases may occur in the future. Any report of dead, sick, or aggressive red foxes in the vicinity of the visitor camp should be investigated without delay.

Davis (1954, pp. 19, 54) reported finding "fox" bones during his excavations of prehistoric village sites at Kukak and Kaguyak. They probably belong to this species since the Arctic fox does not occur here, at least at present.

Canis lupus pambasileus Elliot, Interior Alaska Wolf

In the fall of 1940 all signs indicated that the wolf population west of the Aleutian Range was rather high. By 1953 a decline had taken place here as in many other parts of northwestern North America. However, a good number of wolves persisted in Katmai Monument, and the population at the time of the more recent survey could be described as fair or moderate.

I found tracks or other signs in 1953 at two localities on the south shore of Naknek Lake; around the outlet of Brooks River; on the southwestern shore of Brooks Lake; along Hardscrabble Creek north of Rainbow River; at the north base of Mount Katolinat; on the southwestern shore of the Bay of Islands; on the portage between the Bay of Islands and Grosvenor Lake, and along the lower portion of American Creek.

The following year wolf sign was noted in two places along the north shore of Grosvenor Lake and at the west end of the lake; at four localities on the north shore of Lake Coville; twice near Brooks River; and on the south shores of Naknek Lake and Iliuk Arm.

East of the Aleutian Range, work in 1953 revealed indications of wolves on Cape Douglas, at the heads of Missak Bay and Kuliak Bay, and on Alagogshak Creek. I also saw a den which may have been used by wolves on the southwestern slope of Four-peaked Mountain. W. A.

Davis reported to me that he had seen wolf tracks at Kaguyak during his survey of the area for archeological sites. In general, the data available from the coast of Shelikof Strait indicated a lower population of wolves than on the Bering Sea slope. In the latter section of the Monument I found the highest concentration of wolf sign on the north side of Grosvenor Lake.

Comments of two persons who were acquainted with the area are interesting in connection with the wolf population in 1953. Jay Hammond, a predator-control agent and biologist of the Alaska Game Commission, who was stationed at King Salmon, believed that wolves were decidedly scarce. Alexander J. Fure, who had lived on the north shore of the Bay of Islands since 1916, thought that the animals were numerous. However, he added that they had decreased greatly since 1946-1947 when, in his opinion, the animals were "extremely abundant."

Griggs (1922, p. 315) recorded that he and his assistants came across wolf tracks "occasionally." No mention was made of specific localities except in one instance: "In our first ascent of Katmai Volcano (July 19, 1916), we found the trail of a stray wolf that had passed that way, 2,000 feet up the slope."

In the Katmai area wolves were shy and seen very rarely. Donald Williams, our helicopter pilot in 1953, saw a brownish-gray wolf in the trail about half a mile north of the outlet of Brooks River on September 2. When seen, the animal was standing about 100 feet away. It stared at the man and moved only when he took a few steps in its direction. Then it disappeared at once in the dense willow-alder brush. According to Williams' estimate of its height, "knee-high on a man," it was a rather small animal.

Another wolf was seen about July 6, 1954, by Jean R. Dunn, a biologist who was a temporary employee at the salmon research laboratory of the Fish and Wildlife Service at the outlet of Brooks Lake. This animal was on the road between the laboratory and the outlet of Brooks River into Naknek Lake. The observer described it as gray in color.

I was informed of an incident involving one of this species during the 1952 field season. While camped between the mouth of Savanoski River and Grosvenor Lake, members of the Thirtieth Engineers Base Topographic Battalion killed and cooked a porcupine as a gustatory experiment. Discarded portions of the carcass attracted a wolf into camp, where one of the men shot it.

Most of the wolf droppings found in the course of my work were

examined on the spot for indications of the food habits of the species. In many cases age or nature of the contents prevented identification. In one instance hair of rabbit (*Lepus*) was present. In two others the meals had consisted of ground squirrels (*Spermophilus undulatus ablusus*). Jay Hammond told me that of 26 moose that he found dead in the western portion of the Monument early in January, 1954, only "a few" appeared to have been killed by wolves. Most of the carcasses showed no evidence of predation.

Roy Fure, who trapped in the region for many years, gave an interesting account of wolf predation on lynx. Late on a very cold winter afternoon he came on three wolves that had treed one of these cats. Taking the animals by surprise, Fure shot and killed two of the wolves but the third escaped unharmed. Taking the carcasses on his sled to skin out at his cabin, he left the lynx still in the tree. On returning the following morning, he found the remains of the cat near the foot of the tree, with footprints of a single wolf in the snow around it. According to the trapper's interpretation, the surviving member of the wolf team had returned in time to keep the lynx treed until it was so benumbed by cold that it fell to the ground and could be killed. Fure believed that this type of hunting was not unusual.

Bones of a large *Canis*, which was either wolf or dog, were excavated by Oswalt from the archeological site in Kafia Bay. The remains, which were identified by C. O. Handley, Jr., division of mammals, U. S. National Museum, consisted of two scapulas, two innominate bones, and one tibia. Oswalt (1955, p. 34) assumed these bones to be those of a dog.

Museum specimens of the wolf are not available from Katmai Monument or immediate vicinity, so specific information on the size or other characters cannot be given. Luntley obtained measurements of an especially large track in damp sand on the north shore of Grosvenor Lake, July 11, 1954. The print was $5\frac{1}{2}$ inches long and $4\frac{3}{4}$ inches wide at the broadest point.

There was no indication that wolves in the Monument were exceeding their biological function of aiding in maintaining a normal relationship between other mammalian species and the vegetation. It is to be expected, however, that as long as wolves exist in the area, recommendations will be made from time to time that they be extirpated. The National Park Service has, correctly, given full protection to the species within the Monument. This may not ensure, however, that a "normal" population will be maintained. It is probable that wolf numbers can be reduced by action entirely outside of the sanctuary.

An employee of the Fish and Wildlife Service expressed the opinion to me in September 1953 that poisoning northwest and southwest of Naknek Lake during the previous winter had been "beneficial" in draining some of the wolves from Katmai National Monument.

Lynx canadensis canadensis Kerr, Lynx

The Katmai area has only one representative of the cat family, the lynx. We found it numerous on the Bering Sea slope during 1953 and 1954. The species was comparatively abundant, despite a scarcity of snowshoe hares in 1953 and only a moderate population the following year. I obtained only one record of the lynx east of the Aleutian Range—tracks were found on the pumice flat at the head of Misak Bay, July 24, 1953.

Lynx sign was abundant along lower Brooks River and the adjacent beach of Naknek Lake throughout both seasons of the Katmai Project. Animals were seen there on several occasions: June 29 and three dates in late July and early August, 1953, by Peters; in mid-July, 1954, by Ward; and on August 18, 24, and 30, 1954, by Brody.

I found tracks at numerous other localities west of the Aleutian Range as follows: Western shore of Brooks Lake, June 30, 1953; east of Brooks Lake (3 localities), August 31, 1954; north shore of Iliuk Arm, September 1, 1954; north base of Mount Katolinat, August 21, 1954; Ukak River delta, July 17, 1953, and west bank of lower Ukak River, August 2, 1954; and Hardscrabble Creek, August 19, 1953. Tracks that were probably also those of a lynx were found July 16, 1953, on the two gull islands in Iliuk Arm 100 yards off the south shore. In addition, single animals were observed by Schaller and by me on the south shore of the Bay of Islands, August 15, 1954, and by John Greenbank on the shore of a large lake east of the Bay of Islands, August 22, 1954. The altitude of the localities where the species was recorded in the Monument ranged from near sea level to 500 feet.

When first seen, the lynx that Schaller and I watched was sitting on its haunches on the sandy beach about 6 feet from the edge of the Bay of Islands. It watched us as we moved slowly toward it in our skiff, and crouched when we were about 200 feet away. At 75 feet the boat grounded in shallow water. After watching several minutes longer, the cat arose by a single movement which consisted of straightening its legs. It turned unhurriedly and walked away west along the beach. I noticed particularly the thin, almost emaciated, appearance of the hindquarters. The swaying movement of the rear was marked; at times the body seemed so far off balance on the long

hind legs that I would not have been surprised to see the animal topple over. Seeming not to watch us, the lynx continued to walk along the sand, once quickening to a trot for a few steps, until it turned into the alders nearly 200 yards away. In addition to the long legs other noticeable features were the erectness of the posture, the rich brown color, and the large feet. The tracks were much broader than long and the toe prints were widely separated.

The animal reported by Greenbank was similarly unalarmed. It permitted him to approach in a boat to a distance of 30 feet. In this case the cat may have gained some assurance by being in grass which partially obscured it from view.

In August 1954 a lynx made frequent "patrols" along the south shore of Naknek Lake north of Brooks River, only a few yards from our camp and that of the National Park Service Ranger in charge of the Monument. The cat traveled in a self-made path on the soft sand at the top of the sloping beach, just outside of the grass. Judging by the number of footprints, it must have passed several times during some nights, or the trail was used by more than one animal. The lynx also utilized the human trail that paralleled the shore just inside the edge of the woods. It was seen here one evening by Brody, who called to us in camp a short distance away. At the sound the cat stopped, sat on its haunches, and stared at the man. When he moved away, it left.

This animal, or another one, was encountered by Brody in a wet swale east of lower Brooks River. The creature seemed unconcerned, but when the man moved in to take photographs, it would not allow an approach closer than 75 feet. Then it walked off slowly. A few days later Brody saw a lynx run across the rough footbridge which had been built over Brooks River a quarter of a mile below the falls.

Davis (1954, p. 19) reported finding bone material of this species in his excavation of a prehistoric village site at Kukak.

Eumetopias jubata (Schreber), Northern Sea Lion

The species is included in the list of Katmai mammals on the basis of two badly decomposed carcasses which Schiller (Schiller and Rausch, 1956, p. 200) found on the beach at Kukak Bay in July 1953. The animals were both adult males.

During a flight along the Monument coast about August 1, 1954, Luntley saw in Amalik Bay two large groups of animals which he was certain were sea lions. One herd was on a rocky islet south of Takli Island, the other north or northwest of Takli Island itself. The plane in which Luntley was flying passed over the animals slowly and at

a low altitude. Because of their size he was certain that they were not hair seals—a species with which he was entirely familiar.

C. O. Handley identified three bones, representing at least two individual sea lions, in material excavated by Oswalt from the archeological site in Kafil Bay. A femur was that of an immature animal, while two innominate bones were from an adult or adults. Apparently Oswalt overlooked these remains, as he did not mention the sea lions in his paper. Davis (1954, p. 19) recorded bone material of this species from his excavation at Kukak.

Phoca vitulina richardii (Gray), Pacific Hair Seal

This was by far the most abundant marine mammal on the Katmai coast. Seals were fairly common in the open waters off the headlands and along the exposed shoreline between Cape Douglas and Hallo Bay, but they were more numerous in the sheltered places from Kukak Bay southward. The most populated areas were Katmai, Kinak, Kukak, and Amalik Bays and Geographic Harbor, in the order named.

The presence of small rocky islets at least one-quarter mile offshore was sufficient to draw bands of hair seals. Here the animals could find fish in some numbers and basking places where they were reasonably safe from molestation. In such a situation near the north shore of Kinak Bay I counted about 55 hair seals on July 24, 1953. Three days later we found an estimated 25 animals hauled out on a small rocky island east of the cannery in Kukak Bay.

The long sand bar in Katmai Bay about 200 yards east of the mouth of Katmai River was a favorite resort of this species. In calm weather, when the sand projected a foot or two above high tide, at least a few seals came there whenever the sun provided some warmth. The largest herd of hair seals I have ever seen was congregated here on the morning of October 5, 1940. As we sailed into the quiet lagoon between the bar and mainland beach, hundreds of seals barked at us and swarmed into the water. They swam around our seiner, many coming within a hundred yards, and then dispersed around the ends of the sand bar into Shelikof Strait. For a few minutes my companion and I had to shout to make ourselves understood above the clamor. It was impossible to make a studied approximation of the number of animals present, which may have approached a thousand.

About 97 percent of the bones excavated in 1954 by Oswalt at the archeological site in Kafil Bay belonged to this species. In the large sample examined at the U. S. National Museum by C. O. Handley, Jr., 302 out of 311 bones were those of the hair seal. At least 33 indi-

viduals were represented. A great majority (50 to 80 percent) were immature animals. Davis (1954, pp. 19, 54) also found "seal" bone material in his digs at Kukak and Kaguyak in 1953. Owing to its deteriorated condition, he did not attempt to evaluate it quantitatively or to determine the species.

Oswalt reported the bearded seal (*Erignathus barbatus nauticus*) in his collections from the Kafli Bay site. It was not identified among the 300-odd bones that I saved for later study, and the species is not known to range into Pacific Ocean waters south of the Alaska Peninsula. It has been taken in Bristol Bay, however, and bones could be readily carried across the Peninsula. The appearance of one or two bones of the bearded seal in the midden of the Kafli Bay site is best ascribed to human dispersal, and the species is not included in the list of resident mammals.

Seals are subject to desultory persecution in the bays of the Monument as well as on the open Strait. Commercial fishermen shoot at them because of their supposed destruction of salmon and other valued fish, and other seafarers use them as casual targets. Hair seals are elusive and generally wary, however, and only an expert marksman can kill them with fair regularity. If shooting from airplanes can be prevented, the species will maintain its numbers indefinitely.

Spermophilus undulatus ablusus (Osgood), Arctic Ground Squirrel

This rodent was abundant during both years of the Katmai Project. It ranged from sea level to at least 2,800 feet, the highest point at which I found signs of the species or for which reliable reports are available.

Ground squirrels require low cover and were scarce or absent in areas of dense, tall *Calamagrostis* grass. There were few squirrels, therefore, on the western slope of the Monument below approximately 1,000 feet. East of the Aleutian Range the deep deposit of pumice from the 1912 eruption appeared to favor these rodents by keeping down vegetation. I found them in abundance within 200 feet of sea level in Kukak, Kafli, Missak, Dakavak, and Katmai Bays. In these localities ground squirrels were living on pumice flats or nearly level alluvial fans which were partially covered with low grass, and in clumps or groves of willow, alder, and cottonwood. On such a flat 2 miles from the head of Kukak Bay squirrels had their burrows in hummocks 2 feet high out of which scrub willows grew. They probably resorted to these elevated sites in order to keep above the high water table, for small streams and marshy spots were frequent.

Two exceptions to this sea-level, pumice-flat environment were noted east of the Aleutian Range. Ground squirrels were living in July-August, 1953, on a small ridge about 80 feet high which was far out in Katmai River and about 4 miles north of the shore at Katmai Bay. The steep, rocky island was partially covered with low grass and many flowering herbs, and with alder and willow thickets. It seemed probable that the species here had survived the 1912 ashfall of about 3 feet depth, for restocking by migration appeared unlikely. The nearest (east) bank of the Katmai River was about a mile away, with the intervening space occupied by moving water and churning quicksand.

Another colony of ground squirrels was on a slender peninsula which projected from the south shore of Kafia Bay about three-quarters of the way to the north shore. In addition to rather heavy grass the spit had some dense thickets of alder. The lowest portion of the peninsula, only 10 to 15 feet above the bay, was the site of Oswalt's archeological study and the home of numerous ground squirrels. Oswalt was annoyed considerably by raids of the rodents on his food supplies. He did not find ground squirrel remains in his excavation, but Davis (1954, p. 19) reported them from the Kukak site in 1953.

A number of specimens of the Arctic ground squirrel were collected by Schiller from a colony that occupied the crest of the ridge between Kafia and Kukak Bays. Here, in a saddle about 1,500 feet in altitude, the animals were abundant. Grass and herbs formed a thick ground cover but shrubs were few and stunted. Some of the squirrels from this place carried ticks (*Ixodes angustus* Neumann). (Schiller and Rausch, 1956, p. 197.)

High up on the Aleutian Range Robert Johnsrud and Ronald Kistler made note of ground squirrel colonies that they ran across during explorations July 22-29, 1953, in the southwestern region of the Monument. Many animals were on an east-west ridge of Mount Kejulik at an elevation of 2,000 feet, July 22. At the head of Gas Creek, elevation 2,800 feet, the attention of the men was drawn on July 23 to a green "island" about 20 feet across in an otherwise barren region. The spot was elevated about 2 feet above the surrounding ground and was covered with grass and herbs. It was literally swarming with ground squirrels. On July 24, at 2,200 feet on the unnamed creek east of Gas Creek, a grassy area was riddled with burrows. Squirrels were numerous also, on July 27, at 1,000 feet elevation in the south fork of Martin Creek below Mageik Landslide.

West of the Range most ground squirrels were living in areas more than 1,000 feet above sea level. An exception, which was outside of the Monument, was at 500 feet altitude south of Kulik Lake. There, on September 5, 1953, I found numerous signs of ground squirrels on a north slope covered with mixed grasses and clumps of willow and cottonwoods. I also heard one of these rodents chirp from the luxuriant grassy meadow through which a creek drained Murray Lake into Hammersley Lake (elevation 900 feet). Numerous signs of squirrels occurred in a partly open area where many lichens grew with spruce, willow, and birch at about 500 feet altitude near the south rim of the canyon of American Creek, September 5, 1953.

At higher altitudes ground squirrels were plentiful in 1953: On the grassy tundra at the summit of Mount Dumbling, 2,000 to 2,400 feet, July 10-11; on the tundra at 1,000 to 1,200 feet near the south base of Sugarloaf Mountain, August 17; on low-grass tundra at nearly 2,000 feet northeast of Idavain Lake, August 17 and September 5; among sparse, foot-high grass at 1,700 feet on the ridge west of Douglas River, September 3; on grassy tundra at 2,050 feet between Grosvenor Lake and Murray Lake, September 5; and at the same elevation among grass with patches of willow and alder 2 miles east of the east end of Murray Lake, September 5. The rodents also were found widely distributed over the tundra between Nonvianuk Lake and American Creek below Hammersley Lake. This was high plateau country about 1,000 feet in elevation. It was a few miles north of the Monument boundary in an area that has been proposed as an addition to the sanctuary.

The following year, 1954, ground squirrels were very abundant August 29 on the broad tundra at 1,000 to 1,500 feet elevation north of Idavain Lake. Hardly a minute went by during a two-hour period without our hearing the chirp of one or more of the animals. Squirrels were numerous September 5 on ridges about 1,000 feet above sea level along the south side of Contact Creek. However, the rodents kept strictly to the short-grass areas and did not dig burrows in the depressions where vegetation was luxuriant.

A small colony was found early in August, 1954, in the bottom of the canyon between Knife Peak and Mount Katmai. The animals were living in the steep bluff on either side of the most northeasterly headwater of Knife Creek, in a locality that had been buried under a number of feet of ash during the 1912 eruption. A few small areas were so located that apparently their load of pumice slid off and was carried away by the stream, while avalanches from the slopes above

were split and diverted to each side by rocky promontories. These spots were little gardens of philonotis (a bog moss, *Philonotis fontana*), tickle grass, crisp starwort, mouse-ear chickweed, Arctic poppy, alpine cress, mist maid, and numerous other herbaceous plants. Ground squirrels were living on these "islands" of vegetation in an absolute desert of volcanic ash. Presumably their strain had survived here while all other life had been snuffed out over a wide area roundabout.

Ground squirrels were digging and throwing great quantities of earth from their burrows in the Sugarloaf Mountain region on August 17, 1953. The animals continued active in the Katmai region into early September at least. I heard one or two animals scolding at 1,700 feet altitude east of Douglas River on September 3, 1953, despite the temperature which was in the low forties (F.). My latest record of activity during the Katmai Project was on September 5 (1953) at an elevation of 2,000 feet. In 1940, however, I heard a few squirrels chirping on the upper Ukak River (about 500 feet elevation) as late as the middle of September. How much later they come above ground, I do not know.

One of the most obvious enemies of the ground squirrel in this area is the brown bear. Excavations by bears seeking the rodents in their burrows were common. In walking about 2 miles on the tundra north of Idavain Lake one day at the end of August, 1954, I counted five areas where the ground had been torn up. Most of such holes were relatively shallow, only 1 to 2 feet deep, but occasionally a bear would dig to a depth of 3 feet. Practically all this type of hunting was done in spring or early summer, or late in the fall. Salmon, which were much more easily obtained, took the burden of bear predation off the ground squirrels through July, August, and early September.

Bones and hair of ground squirrels were found in scats of the timber wolf and red fox. The rodents also fall victim to the lynx and wolverine.

Tamiasciurus hudsonicus kenaiensis A. H. Howell, Red Squirrel

The chattering call of the red squirrel was heard frequently in the western lowlands of the Monument wherever white spruce grew. This species of mammal was numerous throughout the two seasons of the Katmai Project. The population appeared to have varied little from that of 1940, but my data for that earlier year were too limited to warrant making a more definite statement.

In the Katmai region, as throughout much of its North American

range, the red squirrel was never seen far from spruce. Mixed coniferous-deciduous woods were acceptable habitat; in fact, I found the species in that vegetation type twice for every occasion that I noted it in pure or nearly pure spruce forest. Seeds of the spruce appeared to be the primary winter food, and one of the best indicators of the presence and abundance of red squirrels was the midden of spruce cones. Great piles of bracts and other discarded parts of cones showed where the animals had had their "tables" during the long winters, and heaps of new cones were added each autumn (pl. 16, fig. 2). On August 31, 1954, I noted east of Brooks Lake that the squirrels were commencing to clip unopened cones from the trees in conspicuous numbers. Twig nests or shelters in the trees also provided evidence of the species' presence.

Localities where red squirrels were found included Brooks River region; south shore of Naknek Lake at three points (2 and 5 miles west, and 1 mile east, of Brooks River); north shore of Naknek Lake; east of Brooks Lake; outlet of Headwaters Creek; Savanoski; west of Grosvenor Lake; Coville River; and two points on the south shore of Lake Coville.

No trace of the species was found in the few isolated groves of Sitka spruce in Kuliak and Kukak Bays, and a careful search of a portion of the Sitka spruce forest on the flats of Hallo Bay was without result. It appeared that this habitat on Shelikof Strait was so thoroughly isolated by physical and environmental barriers that the squirrel had not been able to reach it.

A red squirrel fed through the trees among which we were setting up camp, July 6, 1954, on a spit between Lake Coville and Coville River. The animal appeared to pay no attention to us although we were hammering worktables together and doing other chores. It sought out and tore open occasional curled leaves of the cottonwoods which I assumed contained the larvae of webworms. Most of the bundles were empty and were discarded, but the squirrel ate busily on the contents of several finds.

The red squirrel of the Katmai region is rather dull and pale in color as compared with the subspecies found in eastern North America. An individual that I saw in a spruce grove near the outlet of Headwaters Creek was decidedly yellowish.

Schiller (Schiller and Rausch, 1956, p. 197) collected two female red squirrels near Naknek Lake in 1953. One of these, taken July 8, contained one embryo that measured 30 mm. in length. Both squirrels bore fleas, *Monopsyllus vison* (Baker) and *Orchopeas caedens durus* (Jordan).

Marmota caligata caligata (Eschscholtz), Hoary Marmot

The species has been recorded at Kanatak and Portage Bay (A. H. Howell, 1915, p. 61; Schiller and Rausch, 1956, p. 196). These localities are on the south shore of the Alaska Peninsula and less than 40 miles from the southwestern corner of the Monument at Cape Kubugakli. Therefore we maintained a careful watch for this large rodent, but without conclusive results.

On July 27, 1953, Johnsrud and Kistler saw an animal that corresponded in size and color with this species on the south fork of Martin Creek below the Mageik Landslide. This rocky area at 1,000 feet altitude was the environment in which the marmot would live.

Two days later John B. Lucke and I were pursuing our respective studies on one of the rocky headlands of Cape Douglas when he saw a creature which he was certain was a marmot. The animal was about 200 yards away on a little ridge with some exposed and broken rock, behind which it promptly disappeared. Lucke called to me and we hurried to the spot, but an intensive search revealed no sign of the animal or of a possible den. Dr. Lucke was familiar with marmots in the northern Rocky Mountains and with woodchucks in the northeastern states, and felt positive of his identification.

On the negative side Dr. Werner Juhle told me on August 17, 1953, that he had seen nothing resembling a marmot during the previous two months he had spent in the Monument. Juhle was an exceptionally active geologist who hiked long distances in the Aleutian Range around Mount Katmai, Kaguyak Volcano, and in other areas.

Castor canadensis belugae Taylor, Beaver

Davis found beaver bones in his excavation of village sites at Kukak and Savanoski, but none at Kaguyak where the steep gradients are unfavorable. Among the remains at Savanoski he identified vertebra, pelvis, tibia, and ulna from this species. It was, of course, an item of food as well as wearing apparel for the native people of the region.

Beavers have been abundant and widespread during both periods of time that I have spent in Katmai Monument. Despite poaching that went on almost unchecked late in the 1930's I found little change in the population during my work in 1953-1954 as compared with 1940. Apparently trapping had been local and restricted largely to the regions around Brooks River, the head of Brooks Lake, and the mouth of Savanoski River, and had not made serious inroads before game wardens took a hand.

The species is present on both sides of the Aleutian Range from sea level up to approximately the upper limits of the cottonwood, or about 800 feet. Beavers are not restricted at Katmai to areas where this tree grows, but they do feed on it by preference and in general are associated with it. The large colonies and more dense populations of beavers occurred where cottonwood was prominent. Although beavers sometimes lived in nearly pure stands of alder-willow, they were not numerous there.

Areas of special abundance in 1953 and 1954 were: The grass-marsh-pond country between the lower end of Savanoski River and Grosvenor Lake, and the flats between the base of Mount Katolinat and the lower Ukak River. It appeared that flat, marshy expanses with numerous ponds and sluggish, meandering streams, where the vegetation comprised grasses and sedges, willow, alder, and cottonwood, were optimum habitat.

A few years previous to 1953 beavers had been exceptionally numerous along Hardscrabble Creek up to an elevation of 500 feet, or 10 to 12 miles above the outlet into Grosvenor Lake. When I visited the area in August 1953, dams, lodges, and cuttings were everywhere in the valley bottom along the main stream. The ponds, however, were drained or partially drained, many dams were broken, and comparatively little recent sign could be found. (Pl. 17, fig. 1.)

What had wiped out this large population? Many log jams of cottonwood trees showed that violent floods had swept down the valley during the previous year or two. Perhaps they had dealt the beaver colonies a blow from which they had not recovered. Another or contributing factor may have been the overcrowding with ponds in close proximity for long distances. This may have ended in a disease epidemic which had swept through the crowded population.

Steep gradient, great volume of water, and violent fluctuation in level prevented beavers from establishing dams on the larger streams such as the Ukak and Savanoski Rivers and American and Headwaters Creeks, and on smaller creeks that coursed too swiftly. The gradient factor was especially important on the watersheds that emptied into Shelikof Strait. In some cases, however, large streams became so "braided" and sluggish that the animals were able to maintain a series of ponds on the outermost channels. Such a stream was Rainbow River, the western branches of which were the habitat of numerous beavers. In most cases, however, the larger watercourses supported only occasional lone animals or families that inhabited dens in the banks and probably led a somewhat precarious existence.

Beavers also occupied natural ponds, where they had all the advantages of a stable water level without the labor of building and maintaining the dam. As many of the numerous ponds and small lakes in the western portion of the Monument contained one or more animals, the aggregate population must have been considerable. The animals lived in either bank dens or stick lodges, depending on the topography and size of the water area. If the lake was so large that ice action in spring would be hazardous, the dwelling could be located only in a sheltered bay. Owing to the considerable depth of water in most of the lakes and even small ponds, most lodges were built on or close to shore. This was illustrated on the south shore of Grosvenor Lake, which drops abruptly into deep water. Five lodges were counted in 1954 between the outlet of the lake and the portage to the Bay of Islands, and all were built entirely on shore, with only enough structure projecting into the water to cover the entrances to the living quarters.

I saw few beaver-made structures that are worthy of special mention. As many of the dams were in flat, marshy areas, a moderate height was usually sufficient to create extensive ponds. In such places mud and masses of sod were employed for construction materials in addition to the usual sticks of alder, willow, and cottonwood. These low dams, incidentally, were only minor obstacles for migrating salmon, which usually worked their way over them with ease.

In order to prevent water from escaping around the ends of dams the builders often extended them until they were several hundred feet in length. This low, meandering type of structure was typical of the tundra areas west of the Aleutian Range. One exceptionally high beaver dam that I found at the north base of Mount Katolinat had been built on a small, clear-water creek about 1 mile west of the mouth of Ukak River and a quarter-mile south of Iliuk Arm. Here, on an extensive flat, a pond had been impounded many years previously. The dam was about 8 feet high on its downstream side and, although abandoned and completely covered by grass, was in a good state of preservation with the exception of one narrow section where the stream had broken through. Even the large pond bed was clothed completely in grass, and spruces, willows, and birches about 6 feet tall were taking over.

Another large dam was found in August 1953 on the small, unnamed stream between Ukak River and Ikagluik Creek about a mile above its junction with Savanoski River. Old and abandoned, the structure was about 7 feet high in the middle on its downstream side.

Several lodges were notably large but no precise measurements were

obtained. One of these was in a pond on a small creek immediately upstream from the impoundment back of the large dam mentioned above. Another, even larger, lodge was on the east shore of a circular lake approximately one-quarter mile southeast of the mouth of Brooks River. Its appearance suggested that two adjacent small lodges had been consolidated, making one structure which had settled considerably. The lodge was evidently very old but was occupied when I examined it on July 15, 1953, and had been thickly plastered with mud during the preceding night or two. A house (pl. 17, fig. 1) that I saw in a partially drained pond on upper Hardscrabble Creek on August 19, 1953, was estimated to be about 8 feet in height. This was of much more recent construction than two smaller lodges nearby, which had grass and small willows growing on them.

Judging from the appearance of the dams and lodges, many beaver colonies in the Katmai region have been established for a long time. Some of these old structures are described above. Many lodges that were viewed from the air south of Savanoski River between Iliuk Arm and Rainbow River were partially grass grown. It is possible that these locations had been occupied intermittently, being deserted when the accessible food supply became exhausted and reoccupied after a few years upon growth of the cottonwoods and alders. However, practically all the old lodges that I was able to examine closely on the shore of ponds in the Naknek-Grosvenor-Coville Lakes region were inhabited in 1953-1954. In many cases the preferred types of food were not plentiful, but the animals persisted in staying and from all appearances were thriving.

A dam that I saw in September 1940 at the outlet of the narrow lake about $1\frac{1}{2}$ miles northwest of the mouth of Savanoski River was visited again on August 2, 1954. In the intervening 14 years the dam had been built up by successive generations of beavers although the pond was more than one-half mile long. It was about 6 feet high on the downstream face, its height having been nearly doubled since 1940. Wet mud showed that the occupants of a lodge about 100 yards to the east were busy maintaining it.

No information was obtained on the rate at which beavers reproduce at Katmai. Opportunities for direct observation of the animals were rare, and very few young were seen. Many tracks of young beavers with one or more adults were noted August 19, 1954, on a sandy beach along the northeast side of Iliuk Arm.

A factual item regarding activity in a group of beavers was gathered by Schaller in the course of a night which he spent endeavoring to

photograph wildlife. Late on July 7, 1954, he established himself in a spruce tree near the northwest shore of Grosvenor Lake. Near the foot of the tree was a beaver lodge that opened into a pond. In the otherwise still night Schaller was impressed by the restlessness of the occupants. By the dim light of the near-Arctic summer night he could see them coming and going "almost continually." The animals in the lodge, he reported, were never quiet. They rolled sticks about the floor and kept up a grumbling murmur during the approximately 5 hours that he maintained his position.

Several animals showed much curiosity and fearlessness of man. In a boat, Park Ranger George Peters and I followed a beaver along the shore of Naknek Lake near Brooks River on the evening of June 29, 1953. When we approached too closely, it dived and swam away. However, as we returned to camp and landed on the beach, the beaver followed and cruised slowly back and forth about 30 yards off, watching us. Schiller reported to me that about 10 days later in the same area a beaver approached within 20 feet as he sat in a boat. The following year, on August 14, I had a similar experience. About 4 o'clock on a clear, sunny afternoon I was sitting in the stern of a skiff, the bow of which was aground on the shore of Naknek Lake about 200 yards east of Brooks River. As I watched through binoculars a yellowlegs feeding along the water's edge, a soft, whining "m-m-m" sounded behind me. Turning, I looked down to see an adult beaver swimming by about 4 feet away. The animal was looking up at me, but it continued to swim slowly past parallel to the shore. It continued on, looking about occasionally, until it went from view around a bend in the shoreline.

As mentioned early in this account, cottonwood appears to be the preferred food of the beaver in the Katmai region. My field notes show that in more than 90 percent of the recorded food takings, cottonwood was the sole species. Other foods were taken occasionally, however, either from choice or necessity. Alder seemed to be eaten rarely, while willow was used more often. I found that small willows were being cut in mid-August, 1953, on Hardscrabble Creek, where an ample supply of cottonwood was available. At higher elevations, where the preferred food did not grow, willow seemed to be the principal woody food. On the great marshy flats north of the east end of Iliuk Arm, for instance, several beaver lodges were long distances from cottonwood groves. Here willow and alder were the only usable winter foods. Near the delta of Ukak River, on the lower slope of Mount Katolinat, the beavers in 1954 were depending chiefly on small willows.

As a rule, only trees cut by the beavers themselves are utilized as food. On Hardscrabble Creek in mid-August, 1953, however, the animals were cutting up the limbs and smaller trunks of cottonwoods that had been uprooted and swept downstream in a flood that seemed to have occurred several weeks previously. The trees had lodged in masses here and there on the stream, providing a vast quantity of green food. Some of the cutting was done by beavers that lived in the banks where Hardscrabble Creek had cut into the cottonwood-covered "islands" in the braided stream.

Do beavers find that distant pastures are greener? They show a marked preference for particular cottonwood trees and sometimes go some distance for food even when the same type is close at home. An example of this trait was noted July 22, 1954, near the eastern end of Grosvenor Lake. Beavers that inhabited good-sized lodges on the southwest shore of a large island were felling cottonwoods in groves nearby, but they also were cutting trees on the mainland and towing the pieces 200 to 300 yards across the channel.

Some "skidroads," or trails where beavers drag pieces of wood to water, are so deeply worn that the traces persist for years after the animals leave the area. Near the northwestern shore of Grosvenor Lake a colony of beavers had completely utilized all the cottonwoods and then abandoned the site. In July 1954 darkening of the stumps indicated that the last trees had been cut at least three years previously. Nevertheless, numerous trails where the logs and other portions had been dragged to the water's edge were clearly discernible in the grass.

With man practically eliminated as a poacher in Katmai National Monument, the beaver's mammalian enemies are chiefly the brown bear, timber wolf, lynx, wolverine, and possibly red fox (which may catch a young beaver occasionally). No direct evidence against any of these carnivores was obtained. In two instances holes had been broken in the roofs of two lodges, but in both cases too much time had elapsed for signs of the enemy to persist. One lodge on the lower Ukak River had been broken in two places several years before I saw it on August 2, 1954. A more recent instance was found July 12, 1954, on the north shore of Grosvenor Lake. A hole 12 to 15 inches in diameter had been made through the side of the roof, probably during the previous autumn or early winter. Nearby in the water the willow twigs in the upper portion of an unused food pile were sprouting. The relatively small size of the hole in this lodge indicated that a wolf or lynx was a more likely perpetrator than a bear. It is assumed that the latter would have made a larger opening and scattered the roof material more widely.

Among the mammals that may benefit from the activities of the beaver, or which use the habitat created by the beaver, are moose, otter, mink, weasel, and muskrat. The moose may swim in the pond when seeking relief from heat and insects, and feed on the aquatic plants that develop in the pond as conditions become suitable for them. The otter often finds the pond, or a series of ponds, an easy highway for travel and a refuge from nonaquatic enemies. In the Katmai area the beaver pond is good habitat for the Dolly Varden trout, which is a favorite food of otters. The mink likewise finds fish and perhaps other food in the pond, while the weasel often uses the dam for a hunting ground and a place of refuge. To the muskrat, the beaver pond is excellent habitat and a source of vegetable food.

In the mud of partially drained beaver ponds on Hardscrabble Creek, on August 19, 1953, I found numerous lynx tracks. In the slough formed by a series of ponds a wolf had walked down the valley, crossing the dams in the worn depressions which the beavers had formed in moving from one pond to another.

Waterfowl and some other birds use beaver ponds in spring, summer, and autumn. For example, most large ponds with at least a few dead trees are usually the home, resting places, or nurseries for several mallards, scaups, and goldeneyes, as well as other ducks such as green-winged teals. Loons, cormorants, gulls, and terns often feed in the ponds, and swallows are attracted by the insects that hover above the water. Beaver ponds with a fringe of drowned trees are the favorite resort of the rusty blackbird.

In the summer of 1953 commercial salmon fishermen on the Alaska Peninsula charged that beavers had become so numerous that they had seriously affected the rearing capacity of a number of streams tributary to Naknek and Brooks Lakes. The recommended remedy was reduction of the beaver population by trapping.

I was unable to find evidence which would lend substantial support to this assertion. It is probably true that, with the elimination of trapping, beavers have increased in numbers within the Monument. As the acreage in beaver ponds became larger, it is possible that some gravel beds in the smaller spawning streams became covered with silt and thus less accessible for the reception of eggs. A light covering of silt would not be likely to deter the salmon, however, because they are quite capable of clearing areas down to the gravel. Furthermore, some compensation might result through retention by upstream ponds of silt which otherwise might be washed into the larger lakes and cover those gravel beds which are also useful as spawning grounds.

The chief argument against the beaver as an "enemy" of salmon

is that the dams are alleged to be serious obstacles for the mature fish as they migrate to the headwaters to spawn. I know of no beaver dam in Katmai National Monument that is capable of holding up salmon for any length of time. The larger and more watertight the dam, the easier it is surmounted. Salmon are extremely agile and adept at taking advantage of irregularities in the stream bottom, and the many branches that are interlaced in the front of the typical dam offer innumerable holds for the fish. It should be remembered also that a beaver dam of any height has a sloping face and is not a sheer or even undercut wall like a natural rock waterfall. The salmon is not forced to make a clean leap to the top; it can scramble up the sloping front with its many "fin-holds." The larger beaver dam is comparable to a steep cascade rather than to a typical waterfall.

The small beaver dam that rises only 1 or 2 feet sometimes baffles the migrating salmon for a longer time than the higher dams. The low dam is usually less consolidated and more porous, and the water may pour through in numerous places near the base rather than over the top. Since the fish instinctively heads into the maximum flowage, it may for a time butt ineffectively into the crevices where the water spurts fastest and in largest quantities. However, all but the unusually luckless or the weakest salmon eventually find their way over these lower obstacles also.

The commercial salmon industry has long been seeking escape from its difficulties and has attempted to blame wildlife for the decline of the salmon catch. Among the numerous species "indicted" have been the bald eagle, gulls and terns, cormorants, herons, seals (especially the hair seal), sea lion, otter, and brown bear. It is unlikely that the beaver can be held accountable for any significant loss of reproductive capacity in the salmon resource.

Synaptomys borealis dalli Merriam, Dall Lemming Mouse

Two specimens were taken in the Monument by Schiller (Schiller and Rausch, 1956, p. 197) in July and early August, 1953. One animal was trapped in a sedge-rush-*Equisetum* marsh about 1 mile north of the outlet of Brooks River, at an altitude of 100 feet. The second was taken on a grassy pumice slope on the ridgetop south of Kukak Bay at an elevation of about 1,500 feet.

Clethrionomys rutilus dawsoni (Merriam), Tundra Red-backed Mouse

Red-backed mice and meadow mice (*Microtus*) were abundant in the grassland, with clumps of alder and willow, around the abandoned

cannery in Kukak Bay during midsummer of 1953. It was only rarely that at least one mouse did not appear in any area of about 25 square feet within 10 seconds' time. Snap traps sometimes yielded catches less than 5 minutes after being placed in the grass. Burrows and runways probably made by this species were numerous on a sandy flat at the head of Missak Bay, in grass and other herbs on Kuikpalik Island, and on a grass- and alder-covered rocky hill in lower Katmai River.

In contrast, red-backed mice were rather scarce on the west side of the Aleutian Range during the same season. Considerable trapping by Schiller at Brooks River and at Savanoski yielded only 12 animals in about 10 days.

Microtus oeconomus kadiacensis Merriam, Tundra Meadow Mouse

M. pennsylvanicus alcorni Baker, Alcorn Meadow Mouse

Tundra meadow mice were very abundant along the coast of Shelikof Strait during the summer of 1953, particularly in Katmai, Missak, and Kukak Bays and on Kuikpalik Island. Here they were associated with a large population of tundra red-backed mice. However, around the cannery at Kukak Bay *Microtus* outnumbered *Clethrionomys* in the ratio of more than four to one. The two species swarmed in the grass-fireweed community around the old buildings and the clumps of alders and willows.

On the Bering Sea slope both species of voles were scarce in 1953 and meadow mice were found only at Savanoski Village site. Here Schiller (Schiller and Rausch, 1956, p. 198) trapped seven tundra meadow mice in 1,440 trap-nights.

The following year meadow mice were much more numerous at Savanoski, where on June 30 I saw four or five animals in a few minutes. Twigs with leaves attached had been clipped from low willows along a stream; I attributed the work to these rodents. Mouse droppings were abundant around the wreckage of our food cache, which had been broken into the previous fall by brown bears. Here the rodents had lived well on the "crumbs" and residue which adhered to the many tins that had been chewed or ripped open. I also found mouse signs abundant in 1954 at other points on the western slope: East bank of Brooks River, south shore of Iliuk Arm, on an island in northwestern Iliuk Arm and an islet in the Bay of Islands, at numerous points around Grosvenor and Coville Lakes, and on the tundra at 1,000 feet elevation between Idavain Lake and Sugarloaf Mountain.

During the same summer (1954) voles had become scarce along Shelikof Strait.

Based on these records, the altitudinal range of the tundra meadow mouse within the Monument is sea level to 1,500 feet. The habitat preference is dry grassland.

Three Alcorn meadow mice were trapped by Schiller (Schiller and Rausch, 1956, p. 198) in a sedge-*Equisetum* marsh at the north base of Mount Dumlup about 1 mile north of the outlet of Brooks River. Here they were associated with a small population of dusky shrews (*Sorex vagrans shumaginensis*) and lemming mice (*Synaptomys borealis dalli*).

Ondatra zibethicus zalophus (Hollister), Muskrat

For reasons unknown the muskrat is rare in Katmai National Monument. I saw very few signs of it in the western lowlands and none east of the Aleutian Range along Shelikof Strait. Two animals were seen on the evening of September 8, 1953, swimming in Headwaters Creek near the western boundary of the Monument.

Schiller (Schiller and Rausch, 1956, p. 199) saw only two muskrats at Becharof Lake in the spring of 1954, but said that the natives found "many" there and in Ugashik Lakes. Osgood (1904, p. 25) recorded that the species was common around Becharof Lake when he was there in 1901.

Zapus hudsonius alascensis Merriam, Northern Jumping Mouse

To the extent that limited trapping and few specimens are indicative, the jumping mouse occurs only on the western or Bering Sea drainage of the Monument. It lives in sedge-rush marshes and on the tundra, but is most abundant in the mixed *Calamagrostis*-alder-spruce community. The altitudinal range is wide—from 50 to at least 2,000 feet.

Six specimens were taken in July 1953. (Schiller and Rausch, 1956, pp. 198-199.) One was captured beside a small stream in a moist, grassy swale near the summit of Mount Dumlup, one in a marsh about 1 mile north of the outlet of Brooks River, and four in the rank grass on an old sand dune near the mouth of Savanoski River. Three of the latter, trapped July 18 and 19, were molting heavily on the head and back.

Osgood, in 1902, recorded jumping mice beyond the limit of trees at Cold Bay (now Puale Bay) and also at numerous points some

distance north and northwest of the present Monument. In all instances he found them on moist ground in tall grass or sedge.

Erethizon dorsatum myops Merriam, Porcupine

The type locality of this subspecies of porcupine is Portage Bay, only 40 miles southwest of our area near the south shore of the Alaska Peninsula. The animal appears to be very scarce and is probably local in distribution within Katmai National Monument. Although I watched carefully for signs such as scars on conifers, I failed to find them anywhere in the area. The porcupine is almost certainly present, however, according to the following account.

In conversation on August 13, 1953, with a member of the Thirtieth Engineers Base Topographic Battalion known to me only as Neumann, he told me he had taken part in mapping portions of the Monument during the 1952 season. He said he had seen "a couple" of porcupines in the area between the mouth of the Savanoski River and Grosvenor Lake. Another member of the party had shot one of the animals in order to experiment with wildlife cookery. The carcass was brought to camp, where the skin, head, and other discarded parts attracted a wolf. Because of the circumstances that were related, as well as the unmistakable characters of the species, it seems safe to accept the report as reliable.

A femur of a porcupine was among bones at the archeological site in Kafia Bay that was excavated by Oswalt in 1954. Identification was made by C. O. Handley, Jr. Davis (1954, p. 19) also reported porcupine bone material from his dig at Kukak in 1953.

A number of occurrences of porcupine have been recorded farther out on the Alaska Peninsula from Becharof Lake to False Pass.

Lepus americanus dalli Merriam, Varying Hare

According to Miller and Kellogg (1955, p. 149), on the lower Yukon the varying hare ranges from near sea level up to about 2,000 feet on the adjacent mountains. At Katmai I found the species just back of the beaches on Shelikof Strait and on up to an elevation of 500 feet north of the North Arm of Naknek Lake. Above this altitude in the Katmai region shrub vegetation becomes restricted in area and probably too discontinuous to afford adequate shelter for a forest-dwelling mammal such as the varying hare.

Within its altitudinal range the varying hare seemed to have little preference among most of the forest and shrub types. It was found

in mature spruce forest (which in that region is open with hardwood shrubs interspersed), cottonwood groves, mixed stands, and in thickets of alder and willow. The largest concentrations of signs, however, occurred in scrubby young growth of mixed birch, willow, cottonwood, and spruce. This seemed to afford the optimum combination of food and shelter.

Geographically, the "rabbit" was widespread in the Monument. Its runways, pellets, and characteristic cuttings were found along the eastern foot of the Aleutian Mountains and from their western base to the west and north boundaries of the Monument. I recorded it as abundant or numerous around Missak Bay, on a rocky knoll in lower Katmai River, along the south shore of Naknek Lake and western end of Iliuk Arm, and from the northern shore of the North Arm of Naknek Lake north around Lake Coville and the west half of Grosvenor Lake. Extraordinarily heavy feeding had occurred in places within the latter region, notably near the south shore of Lake Coville 3 miles west of Coville River, south of the westernmost 3 miles of Grosvenor Lake, and immediately north of Coville River. Rabbits were also very abundant near the outlet of Brooks Lake. On the other hand, markedly sparse populations were noted in Hallo Bay, along the eastern shore of Grosvenor Lake (east of the portage to the Bay of Islands), and on Kuikpalik Island in Shelikof Strait.

Kuikpalik Island is 2 miles off the nearest point on the mainland. In view of the cold and stormy character of the intervening waters, as well as the scarcity of tree growth on the islands, it was a little surprising to find a few hare pellets here and there in the grass. A fox dropping also found was made up largely of fine white hair which could only have come from a hare in winter coat. The species may have reached this isolated outpost when glacial ice extended to it from the mainland, or on floating ice from tidewater glaciers. It is also possible that "rabbits" were introduced deliberately as food for free-ranging foxes when Kuikpalik Island was utilized as a fur ranch during the 1920's.

On inland lakes half a mile of open expanse was no deterrent to hares in making their way to islands. This travel was accomplished, of course, during the winter months when the lakes were frozen over. One of the densest populations of hares in 1954 was found on two small, steeply sloping islands in the northeastern end of the Bay of Islands. Sand beaches around one of the islets showed many fox tracks; the foxes may have been attracted by the large food supply.

Signs of varying hare, as well as ground squirrel, red fox, and

mouse, were seen July 28, 1953, on an "island" in the lower valley of Katmai River. This rocky knoll, which was well covered by grasses, willow, and alder, was surrounded by the churning, braided courses of the river. Separated from thickets on the valley margins by at least a mile of open bars and many streams of rushing, silt-laden water, this 5- to 10-acre patch of ground appeared to be quite inaccessible to any of these rodents.

The hare population of the Monument was distinctly higher in 1954 than during the previous year. The cycle was seemingly near its peak or, in some localities, may have passed the maximum. For instance, the cutting of birch and other shrubs on the hills immediately west of Grosvenor Lake had been most intensive in the winters of 1952-1953 and 1953-1954, but the number of animals flushed in this area during July 1954 was comparatively small. A die-off may have occurred during the second winter or, more likely, the spring of 1954. South of Grosvenor Lake, however, the population was still high in July 1954. Schaller counted 12 hares in about 8 hours of hiking on July 13 in this locality, between the outlet of Coville River and the north shore of the Bay of Islands. The birch and mixed birch-willow thickets were so dense that walking was very difficult, and the number of animals actually seen must have been reduced correspondingly. A dozen sight records in this type of cover indicated a large population.

The winter food appeared to consist largely of the buds, twigs, and young shoots of Kenai birch (*Betula kенаica*). The entire plant down to a diameter of about one-eighth inch was eaten. Bark of larger stems, up to 2 or 3 inches in diameter, was nibbled off with the incisor teeth, but this type of food was definitely secondary to the twigs and shoots. In places practically all birch stems of the younger age-classes had been nipped off at snow level over several acres in extent. On the moraine that bordered the southeastern shore of Naknek Lake birch twigs had been clipped 4 feet above the ground. The snow depth here had been 2½ or 3 feet.

For a time I was puzzled by finding many cuttings consisting of the upper portions of the plant and clusters of single leaves of fireweed (*Epilobium angustifolium*). These fragments were numerous at some places in the lake region of the Monument during August 1954. Some were freshly cut; others were wilted but still identifiable a week or more after clipping. Most were in or alongside trails that showed current use by rabbits. Finally, I found the lower portion of a plant from which only a few leaves had been removed when, perhaps, the diner had been interrupted and frightened away. The base of this

stem plainly showed the marks of rabbit teeth. Apparently, the varying hare relished most the lower, tougher portion of the plant but discarded the leaves and, sometimes, the terminal 3 to 4 inches of the stem. I did not notice any use of fireweed before approximately August 5, when the stems may have been too immature to suit the animals' taste.

A small garden near the Brooks Lake salmon research laboratory of the Fish and Wildlife Service furnished little food to the scientists but was enjoyed by hares which were numerous in the vicinity. As I passed the garden on September 1, 1954, I found that these animals had completely devoured the foliage and stems of the stunted turnips, broccoli, radishes, and lettuce. Only carrots had been ignored.

With the rabbit at or near peak numbers, one could expect to find evidences of mortality. While die-off conditions on a widespread scale had not been reached, I recorded a rather large number of casualties in 1953 and 1954. Remains of hares were found in fox and wolf droppings. Cause of death usually could not be ascertained, but in two cases it was fairly certain that owls had made killings. In one of these instances we heard a hare scream about midnight on July 12, 1953, near our camp about a mile north of the mouth of Brooks River. The remains (four legs and part of the skin) of a juvenile hare were found the following morning in the trail back of camp. A large owl (almost certainly the horned owl, *Bubo virginianus*) had been flying on short forays near the spot immediately before the death scream sounded.

Other potential enemies of the hare in the Katmai area included the great gray owl (*Strix nebulosa nebulosa*), snowy owl (*Nyctea scandiaca*), Peale's peregrine (*Falco peregrinus*), marten (*Martes americana*), short-tailed weasel (*Mustela erminea*), mink (*Mustela vison*), and lynx (*Lynx canadensis*). The latter species, which depends heavily on hares when the latter are abundant, was numerous in 1953-1954.

A few incidental observations made in 1954 are worth recording here. The first occurred about 9 a.m. July 7, when an adult varying hare came into our camp area on the eastern shore of Lake Coville. Although my companion and I were moving about and talking, the animal continued to hop along on a fairly direct course that took it within 20 feet of the cook tent. It paused every few feet to bite off herbs which it chewed and swallowed, and occasionally to look at us with apparent lack of alarm or interest when we made a particularly abrupt movement.

Around midday of August 19 I was repairing a skiff on the open, sandy beach of Naknek Lake west of Brooks River when an immature but well-grown hare came out of the alder-willow shrubs and turned parallel to the shore. It ran (not hopped) at a rate hardly faster than a man's walk. As it kept on west along the beach for a hundred feet before turning into the woods, I noticed particularly that the hind legs were so long that the effect was amusing. This stretch of beach where the rabbit rambled so unconcernedly was patrolled frequently by one or more lynxes.

Three days later, about 11 p.m., Brody opened the zippered door of our cook tent and started to step out. Immediately a young hare about 8 inches long hopped over his foot and into the tent. The animal was caught easily and was placed in an empty wooden box without a cover but with sides 18 inches high. The men experimented by offering several kinds of food, none of which interested the hare. After 5 or 10 minutes during which it sat quietly, the hare suddenly sprang upward from a sitting or crouching position and cleared the rim of its "cage." The leap of more than 18 inches, without any evident preparation or effort, seemed extraordinary for such a young animal. The men then opened the door and allowed the hare to return to its normal habitat.

Davis found the mandible of "a rabbit" in excavating at Savanoski during the summer of 1953. Presumably it was that of the varying hare rather than the Arctic hare, which would not have occurred in the vicinity of the site.

Lepus othus poddromus Merriam, Alaskan Arctic Hare

In August 1954 I found droppings of this large hare on the tundra north of Idavain Lake at an elevation of about 1,500 feet. No animals were seen here or elsewhere, however. The species is probably limited within the Monument to the extreme western portions beyond the altitudinal or other limits of woodland. The larger areas of open tundra, suitable for Arctic hare, are the high country between Idavain Lake and Sugarloaf Mountain, the region south of Brooks Lake, and the drainage of Angle Creek. Hares probably do not occur in the Monument east of the Aleutian Range, where their habitat is extremely limited.

Arctic hares were said to be abundant around Becharof Lake, west of the Monument, in the winter of 1953-1954. Schiller (Schiller and Rausch, 1956, p. 196) saw them there in May 1954 and collected a female weighing 5.5 kg. on May 16.

Alces alces gigas Miller, Alaska Moose

This magnificent animal, the largest of all the moose, is numerous in the Monument. Katmai is the only sanctuary for the species on the Alaska Peninsula, which is one of the noted hunting regions in the State. Thus the Monument is one of the few places, together with Mount McKinley National Park, where visitors are almost certain to see moose undisturbed in their primeval setting.

Prior to establishment of the Monument the moose was an important source of food for the native people. Davis (1954, pp. 19, 54) identified its bones in material from his excavations at Kukak and Kaguyak. Ribs found in the diggings at Savanoski were termed those of "large cervidae" (pp. 60-61) but they probably included remains of moose. The older and smaller village site in Kafkia Bay which was excavated in 1954 by Oswalt yielded only one badly eroded metacarpel or metatarsal bone of a hoofed mammal. This was identified tentatively by Handley as being caribou, but with the provision that it may have been from a young moose. As the moose is a comparative newcomer to the Peninsula, it may have been scarce or nonexistent in the region of Kafkia Bay before the Russian occupation.

For several decades early in the twentieth century moose had been rather scarce on the base of the Alaska Peninsula. This may have resulted from overhunting by the natives, for Osgood (1904, p. 29) quotes a report that nearly 20 moose had been killed in the vicinity of the Naknek River during the spring of 1903. At the time of my first visit to Katmai in September 1940 residents of Naknek told me that moose had begun to appear occasionally near the village for the first time in many years. These animals were thought to be coming from the National Monument or its immediate vicinity, where they were plentiful. I saw many tracks at that time near Brooks River, Brooks Lake, and around the eastern end of Iliuk Arm. During some three weeks of travel I observed at least a dozen animals west of the Aleutian Range.

Moose were still numerous in the Monument when I returned in 1953, although they may have been somewhat less abundant than during 1940. Early in the 1954 season a reduction in sight observations and track records indicated an apparent downward trend in the population. This was partially offset, however, by an increase in sight records later in the summer.

The species is widely distributed in the Monument, and signs may be found almost anywhere below the permanent snowline. The regions

of greatest abundance in 1953-1954 were the mixed spruce-birch-cottonwood forests and alder-willow thickets of the lakes region and similar habitat in the lower valleys back of Hallo, Kukak, and Katmai Bays. Moose usually could be seen in the extensive marshes with scattered groves of cottonwoods, alders, and willows between the Bay of Islands and the eastern portion of Grosvenor Lake.

Lone animals, generally bulls, wandered about the open tundra above timberline and west of the forest limits. The rolling plains in the western part of the Monument were used especially in autumn. This area was not true tundra but was dotted with clumps and patches of willow, birch, alder, and stunted spruce. The first-named shrub is the staple food. At higher elevations moose occurred more infrequently and erratically. I found tracks and other sign early in July, 1953, along a small stream just below the summit of Mount Dumlupınar (2,440 feet elevation). On September 5, 1953, I saw a cow moose swimming from north to south near the middle of Murray Lake, which is 1,599 feet above sea level. Johnsrud and Kistler, who were assistants in geology studies during 1953, told me that they saw tracks at 2,500 feet elevation in an area immediately south of Kejulik Pass that was completely barren of vegetation.

Moose occasionally wander into or cross the Valley of Ten Thousand Smokes which is practically devoid of food. In July 1954 I found unmistakable evidence of browsing on the tips of willow shrubs about 3 feet tall that were growing on a gravel knoll a short distance below the glacier in the fork of the two streams that make up the head of Knife Creek. The elevation here was about 2,200 feet. It was astonishing to note this proof of indifference of these huge animals to physical hazards and hardships involved in traveling through such a bleak region. In September 1940 we saw a large bull slowly plodding across the open delta of the Savanoski and Ukak Rivers during a violent gale when the air was filled with pumice. Although we were unable to face the blast for more than a few minutes, the moose continued steadily on his course during the hour or more that he was in sight.

Willow leaves and twigs constitute the staple food, and apparently willow browse makes up the entire winter diet. In summer the moose subsist to some extent on herbaceous plants that are found in marshes and around the margin of lakes. I did not find that aquatic plants were taken in the Katmai region.

Despite the number of animals that browsed it, willow was not used to excess. Snow depths apparently were not excessive, so the

moose could move about easily and find new feeding grounds. No such overbrowsing was evident at Katmai as has been common in Yellowstone National Park and Jackson Hole, Wyo. The most frequented winter ranges in Katmai Monument were the lower Savanoski River, south shore of Iliuk Arm, and north shore of Lake Coville.

As could be expected in a stationary or possibly declining population, comparatively few calves were seen during the period of the Katmai Project. Most of those observed were singles; in fact, only one set of twins was identified as being with a lone cow.

Moose are habitual users of trails, and those at Katmai were no exceptions. The National Geographic Society trail from Iliuk Arm to the Valley of Ten Thousand Smokes was kept open, as late as 1940, by combined travel of moose and brown bears. An old native trail from Naknek Lake to the top of Mount Dumlupning showed fresh tracks of these species on July 10, 1953. I found two trails on August 17, 1954, which paralleled the south shore of Naknek Lake near the west boundary of the Monument and were used by moose and bears. In other places, as east of Brooks Lake and on the moraine between Naknek Lake and Iliuk Arm, moose continued to use trails that apparently had been made and subsequently abandoned by brown bears.

I observed several instances of the rather strong curiosity trait in moose. In late September, 1940, I attempted to obtain photographs of a large bull that was beating his antlers against a dead tree in the woods northwest of the mouth of Savanoski River. When my presence was betrayed by a red squirrel's alarm call, the bull stole off but returned to circle me in almost complete silence. Only an occasional snapping twig revealed his progress as he sought to learn more about the intruder. In June 1953 the fishery biologists at the Brooks River laboratory told me that a moose watched them for several hours on one occasion as they worked counting salmon and taking scales at the weir. A large bull walked out belly-deep on the south shore of Lake Coville on September 2, 1953, to watch Robert Luntz and me as we moved slowly along in our motor-driven dory. The animal obviously was inquisitive.

Moose, especially the bulls, are much more phlegmatic in the presence of aircraft than are brown bears. A large bull stood his ground near the mouth of the Ukak River about July 1, 1953, until we had circled in the helicopter to a point less than 100 feet directly overhead. Only then did he run into dense growth. We passed over a cow with twin calves in a marsh south of Grosvenor Lake on August 16, 1953, at an elevation of 400 feet; the calves stood stock still while the cow

circled to face us with the mane erect on her neck. At about 500 feet elevation we flew over a large bull with two cows in a grassy area east of Idavain Lake on September 6, 1953. Although the cows were nervous and uncertain as to which way to run, the bull continued lying down, undisturbed by the beat of the rotors.

The reaction of a bull moose to a small outboard motor has been described earlier. That animal showed considerable curiosity and no fear. On another occasion, however, I tried to approach a cow at the east end of the Bay of Islands. Although I throttled the motor down to about one-quarter speed, the animal became uneasy and walked, then trotted, out of the water and into the woods.

About a dozen instances of mortality were found during the summers of 1953 and 1954. Only one was a recent death; in fact, most of the remains were more than a year old. In a large population such as existed at Katmai, this incidence of findings is not at all excessive.

A cow moose was found dead August 30, 1953, on the west margin of Brooks River above the falls. Since most of the carcass was in the water and could not be examined satisfactorily, the cause of death went unexplained. It is possible that this animal was killed and left uneaten, at least for the time being, by a salmon-surfeited bear.

A large bull, which apparently had fallen from a cliff on the south shore of Naknek Lake about 1 mile north of Brooks River, was examined on July 7, 1953. The lower jaw and some of the upper teeth had been lost through decay and wave action, but three rear molars remained. They were worn far down and showed evidence of caries. The animal was clearly near the end of its life span when it fell and was killed. Weakness resulting from age and cold may have been a factor in the accident, which had occurred sometime during the previous winter.

The carcass of an exceptionally large cow drifted into the head of Coville River, at the eastern outlet of Lake Coville, early in July, 1954. The animal had been dead at least one month and probably longer. Most of the ribs on one side had been broken out and the entire side and viscera were missing. The condition indicated that the carcass may have been fed upon by wolves as it lay on the ice. It was possible that the animal had been killed by predators or that it was a victim of winter-kill and old age.

Practically all of the skulls that I found at Katmai showed evidence of advanced age. Thus there is nothing in my limited findings to indicate that the apparent downward trend in the population is anything more than a gradual, normal fluctuation. However, a report of con-

siderable mortality in the early winter of 1953-1954 should be recorded here. Jay Hammond, then a warden of the Alaska Game Commission at Naknek, told me that on an airplane patrol prior to January 1, 1954, he counted 26 dead moose in Katmai National Monument. "A few" may have been killed by wolves, but most of the carcasses showed no signs of predation. Hammond broke open the leg bones of some of the animals to check for evidences of starvation, but neither the marrow color nor general physical condition indicated malnutrition.

HYPOTHETICAL LIST

Martes americana keniensis (Elliot), Marten

Petroff (1898, p. 203) stated in 1882 that this furbearer was "plentiful" on the Alaska Peninsula during the Russian occupation, with the implication that it was one of the primary objectives of the native trappers. During my stay in Katmai Monument I did not obtain any information on this beautiful animal. It may have been present in the spruce forest on the western lower slope. The marten was one of the furbearers that Griggs (1922, p. 315) "expected to reappear in force, now that the native villages have been abandoned, leaving the country an uninhabited wilderness with no one to hunt them down." As a matter of fact, trapping was to continue for many years after this prediction was written in 1922.

Enhydra lutris lutris (Linnaeus), Northern Sea Otter

No trace of the sea otter was found along the coast of the Monument. Apparently it was extirpated from this region late in the nineteenth century. According to Petroff (1898, p. 205) it was an important resource locally during the Russian period. The hunters of Katmai village "could have reindeer (i.e., caribou) in plenty by climbing the mountains that rear their snow-covered summits immediately behind them, but they prefer to brave the dangers of the deep and to put up with all the discomfort and inconvenience connected with sea-otter hunting." At the end of the Russian occupation, he recorded that "now Katmai's commercial glory has departed, and its population, consisting of less than 200 creoles and Innuits, depend upon the sea-otter alone for existence." According to the Eleventh Census (Anon., 1893, p. 72), the hunters were forced by 1890 to "journey far from home to find their quarry, and the number of skins brought home grows smaller year by year."

During much of the nineteenth century Kaguyak was one of the centers of otter hunting. The Eleventh (1890) Census, which was published in 1893, stated (p. 72) that, "Formerly this vicinity was looked upon as one of the most important sea-otter hunting grounds, but of late years the trade in these valuable skins at (Kaguyak) has become insignificant, and the natives are obliged to seek distant hunting grounds with the assistance of the traders."

Davis and Leach recovered sea otter bone material from their excavation at Kukak in 1953, and they found a fine "modern" otter spear on the beach nearby. However, Oswalt discovered nothing at the Kafia Bay site to indicate that the inhabitants there had hunted or used the sea otter.

Osgood (1904, p. 47) recorded that, "The coast of the Alaska Peninsula from Iliamna Bay westward was formerly much frequented by sea otters. Kamishak Bay was a favorite hunting ground for the natives of Iliamna Village and others. Even within the past five years (prior to 1902) parties have hunted otters there with considerable success." (The northeastern corner of the Monument now extends to the southern shore of Kamishak Bay.)

Osgood also mentions that a sea otter was shot with a rifle from a bluff near Cold Bay (now Puale Bay), a few miles from the southwestern corner of the Monument, in the winter of 1901-1902. His assistant obtained a skull from a native hunter at Kanatak, but the exact spot where the animal was killed apparently was not ascertained.

As far as is known the coastal environment has undergone no significant change since the time of the fur trade. Without doubt overhunting was responsible for the local extirpation of the sea otter. If the species continues to increase under protection, its reappearance in the Monument will be only a matter of time.

Lemmus trimucronatus minusculus Osgood, Brown Lemming
Dicrostonyx groenlandicus rubricatus (Richardson), Greenland
Collared Lemming

The latter species has been recorded from Nushagak, 80 miles west of the Monument, and from Port Moller on the west coast of the Alaska Peninsula. Schiller (Schiller and Rausch, 1956, p. 197) obtained a specimen in wet tundra near the south arm of Becharof Lake and saw another on the pass between Portage Bay and Lake Ruth. Both of these localities are west of the Monument boundary but in habitats which are similar to the valley of Angle Creek within the Monument.

The brown lemming probably also occurs in the Katmai area. It has been taken northwest of the Monument on the Nushagak River near Kakwok, which is approximately 60 miles from the nearest point on our boundary. It has also been recorded from Chignik, on the east coast of the Alaska Peninsula 165 miles southwest of the Monument.

Callorhinus ursinus cynocephalus (Walbaum), Northern Fur Seal

I have found no evidence that the fur seal now occurs in the waters along the eastern shore of Katmai National Monument. Neither is there anything to indicate that it was ever present in commercial numbers during the Russian occupation. However, the Monument is not far from the migration route of the species, and it is likely that erratic wanderers or storm-driven individuals may come into the bays occasionally.

Schiller (Schiller and Rausch, 1956, p. 200) found the carcass of a young male fur seal on the beach at Kanatak in May 1954. The animal had been washed ashore and had been dead for some time.

Rangifer arcticus granti J. A. Allen, Grant's Caribou

This small, pale subspecies of caribou is restricted to the Alaska Peninsula. Its numbers have been greatly reduced during the past half century and it is now absent from the northern half of its former range, including Katmai Monument.

There is no doubt that the species formerly occurred within the present Monument. The watershed of Angle Creek, the region west of Mount Dumlup, and the area between the North Arm of Naknek Lake and Grosvenor Lake are typical caribou range. The rolling hills covered with grass or low shrubs, with bogs and lakes in the valleys, form a habitat very similar to that around Becharof Lake where Osgood (1904, p. 28) recorded "small herds" in 1902 and 1903. He mentioned one animal which was killed by a prospector in July 1902 "about 15 miles northeast of Cold (now Puale) Bay." The spot appears to be on the headwaters of King Salmon River close to the southwestern boundary of the Monument.

Osgood stated that even at the turn of the century the herds were being killed off rapidly both by whites and natives, and he feared for the survival of the subspecies on the Peninsula unless commercial hunting could be stopped. Apparently this slaughter eliminated the caribou in the Katmai area, for I have been unable to obtain any evidence of their existence in the Monument since its establishment in

1918. This is particularly true of the western tundra which was included within the boundaries as late as 1930.

From the earliest times Grant's caribou undoubtedly was an important factor in the economy of the native people. Petroff (1898, p. 203) wrote in 1882 that, "The reindeer browses and herds all over this region (the Bering Sea slope of the Peninsula), retreating during the summer up to their inaccessible retreats among the snowy peaks of the (Aleutian) mountain range, where they are often seen by the traveler below as a moving line of black dots winding around the summits. During the autumn and winter they seek the vicinity of the lakes and scatter over the tundra, where they are hunted with comparative ease."

The same writer attested that caribou were numerous on the eastern slope of the Aleutian Range at least as far north as the headwaters of Katmai River. Speaking of the people of Katmai Village, he commented that they could take caribou in plenty by climbing the mountains behind the village, but that they preferred to hunt the sea otter, "and in case of success purchase canned meats and fruit from the trading store, leaving the deer on the mountain undisturbed." Compilers of the Eleventh Census (Anon., 1893, p. 72) mentioned that "the more enterprising hunters (of Katmai Village) kill caribou in the mountains."

Davis (1954, p. 19) recovered bone material of caribou from the Kukak and Kaguyak sites. Ribs of "large cervidae" which he excavated at Savanoski (pp. 60-61) may have belonged to caribou or moose, or both. Largely because much of the bone material at these sites was badly decomposed, he did not discuss the relative abundance of caribou in the recoveries.

The caribou was considered by Oswalt to have been of little consequence in the lives of the prehistoric hunters at Kafia Bay. In his "Selected Bone Count" (1955, p. 52) he recorded three long bones of caribou in the midden excavation as compared with 247 seal long bones. He concluded that (p. 43) "these people became almost exclusively seal hunters because of the general paucity of game in the area rather than from failure to utilize the available resources." This need not imply that in olden times caribou did not range northward from the Katmai River drainage. In summer the animals would have stayed high on the slopes of the Aleutian Range where they were quite inaccessible to the natives of Kafia Bay. To obtain snow-free grazing in winter, the bands would have traveled south to the open tundra south of Katmai River rather than to the deep, alder-choked canyons along the shore of Shelikof Strait.

During recent years Grant's caribou have been increasing in population and ranging farther north and east on the Peninsula. The calf crops of 1950-1953 were good and, according to Jay Hammond, then warden of the Alaska Game Commission at Naknek, reproduction was as high as 30 percent. In the summer of 1953 a band of about 20 caribou were reported near Big Creek, approximately 4 miles south of Naknek River and 5 miles southeast of King Salmon Air Force Base. Apparently this was the northernmost occurrence in many years. Roy Fure, one of the oldest residents of the region, told me that since his arrival in 1912 he had never known of any caribou north of Naknek River.

If the upward trend of population continues, it is probable that caribou will once more appear in the western portion of the Monument. Whether the nomadic herds will remain throughout the year is uncertain. Even if they enter only seasonally or irregularly, they will be an interesting and important element of the native wildlife. It is hoped that this niche in the fauna, which has been vacant so long, will be filled once more by natural migration.

Rangifer tarandus (phylarchus Hollister?), Kamchatka Reindeer

This Old World deer from the Siberian coast was introduced to the Alaska Peninsula when herds were driven in from more northern areas of Alaska. It was intended that the herds would furnish supplemental food for the natives, especially in years of poor salmon harvests. This well-intentioned program was not successful, largely because the natives would not practice proper reindeer management. The herds were abandoned during the summer months—the traditional fishing season—and soon dispersed and were lost.

I was told by Jay Hammond that reindeer were numerous in the northwestern part of Katmai National Monument during the period approximately 1925-1935. They decreased rapidly after that time and the survivors disappeared about 1942. Since I did not get into this area during my first visit to the Monument in 1940, I am unable to verify the information that Hammond had received from local residents. However, during a flight over the tundra between Iliamna Lake and Naknek in early September, 1940, I was impressed by the maze of clear-cut trails in some places north and northwest of the Monument. Brush corrals and stone cairns (used in hunting caribou or reindeer) were also seen from the plane. It was evident that reindeer had been numerous in the region within a comparatively few years. The caribou had been extirpated three or four decades earlier.

Evidence of the past presence of reindeer in the northwestern portion of the Monument was plain as late as 1953. On August 17 I made observations along a ridge about 2 miles north of the North Arm of Naknek Lake and 6 miles southeast of the outlet of Idavain Lake. As the elevation was 1,000 feet or more, the vegetation consisted of grasses, blueberry, and crowberry, with occasional clumps of alders and a few lone, stunted spruces. Across this grassland a number of conspicuous trails coursed in a generally east-west direction. In places, for distances varying between 100 and 200 yards, the trails were about 12 inches wide and beaten 2 or 3 inches deep in the mineral soil. Gradually the paths then broke up into narrow footways which diverged several yards from the course and did not cut through the ground cover. Fifteen to thirty yards farther on, the small trails coalesced again. The ridge apparently had been part of a migration route of caribou or a driveway for reindeer—presumably the latter.

Similar trails were evident on an indefinite mountain mass 2,000 feet in elevation 5 to 8 miles southeast of Sugarloaf Mountain. The plant cover was composed of grasses, dwarf willow, blueberry, and crowberry. The trails here also ran in a generally east-west direction. Beside one of the most heavily beaten paths I noticed a weathered object about 3 feet long which resembled a gnarled stick. As trees were completely lacking, I examined the object and found it to be the remains of an antler. (Pl. 17, fig. 2.) The length of the beam was such that it was clearly from either a reindeer or caribou. All palms were missing, probably eaten by Arctic hares or ground squirrels. The beam was split in places so that the interior was filled by fine, windblown soil and by moss. From its weathered appearance, the antler had been shed many years before—possibly before the introduction of reindeer to the region.

Careful search of both of the areas described did not reveal any of the lichens that are preferred as winter food by reindeer and caribou.

Eschrichtius glaucus (Cope), Gray Whale

In his digging at Kafia Bay Oswalt unearthed several bones that probably were those of the gray whale. These remains may have come from a distance. Nevertheless, the species ranges along the coast and, like some of the smaller whales, may come into the bays at times. As a "representative" of the group, the gray whale is added to the hypothetical list with the expectation that it and perhaps other species of whales will eventually become stranded on the Monument.

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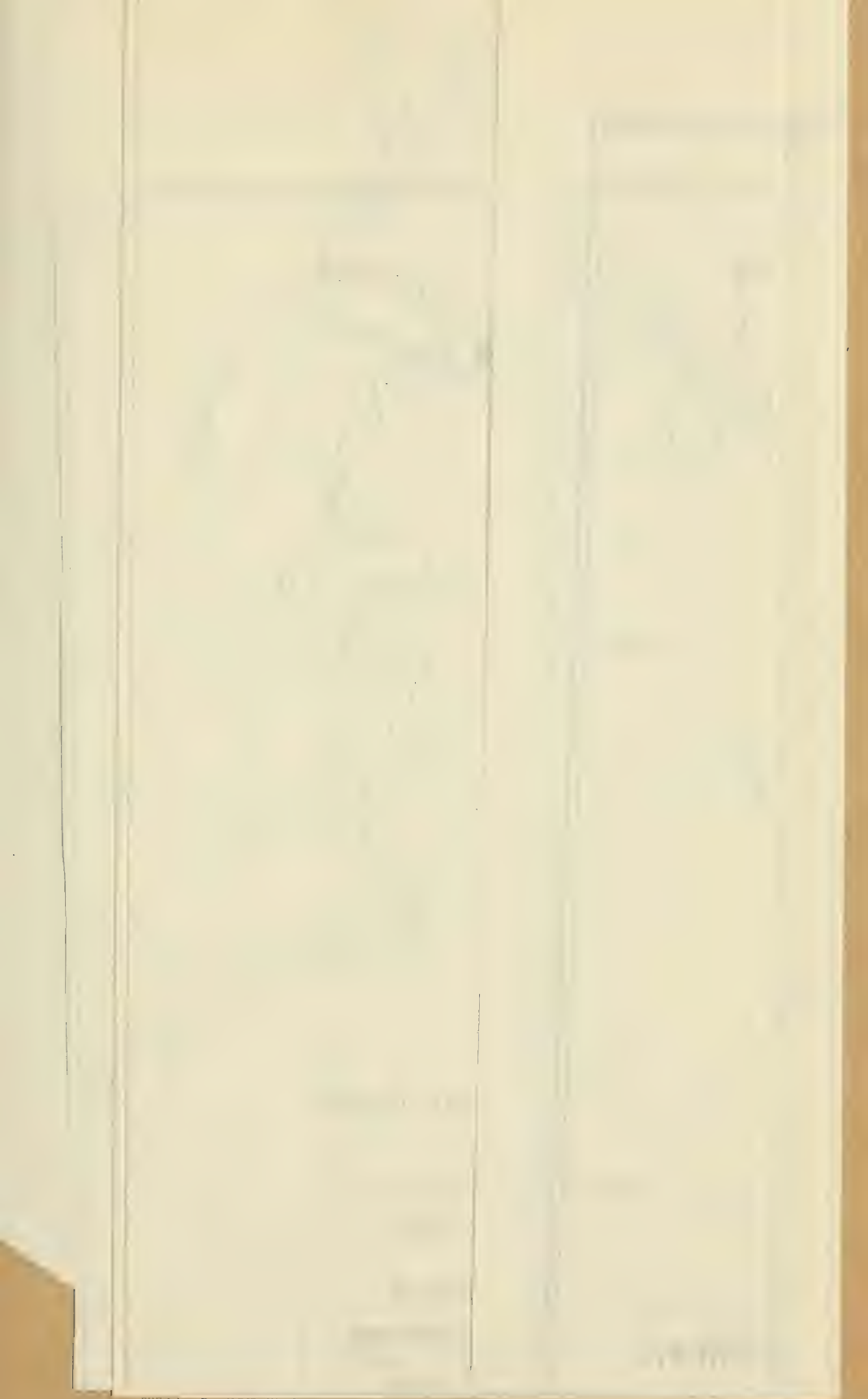
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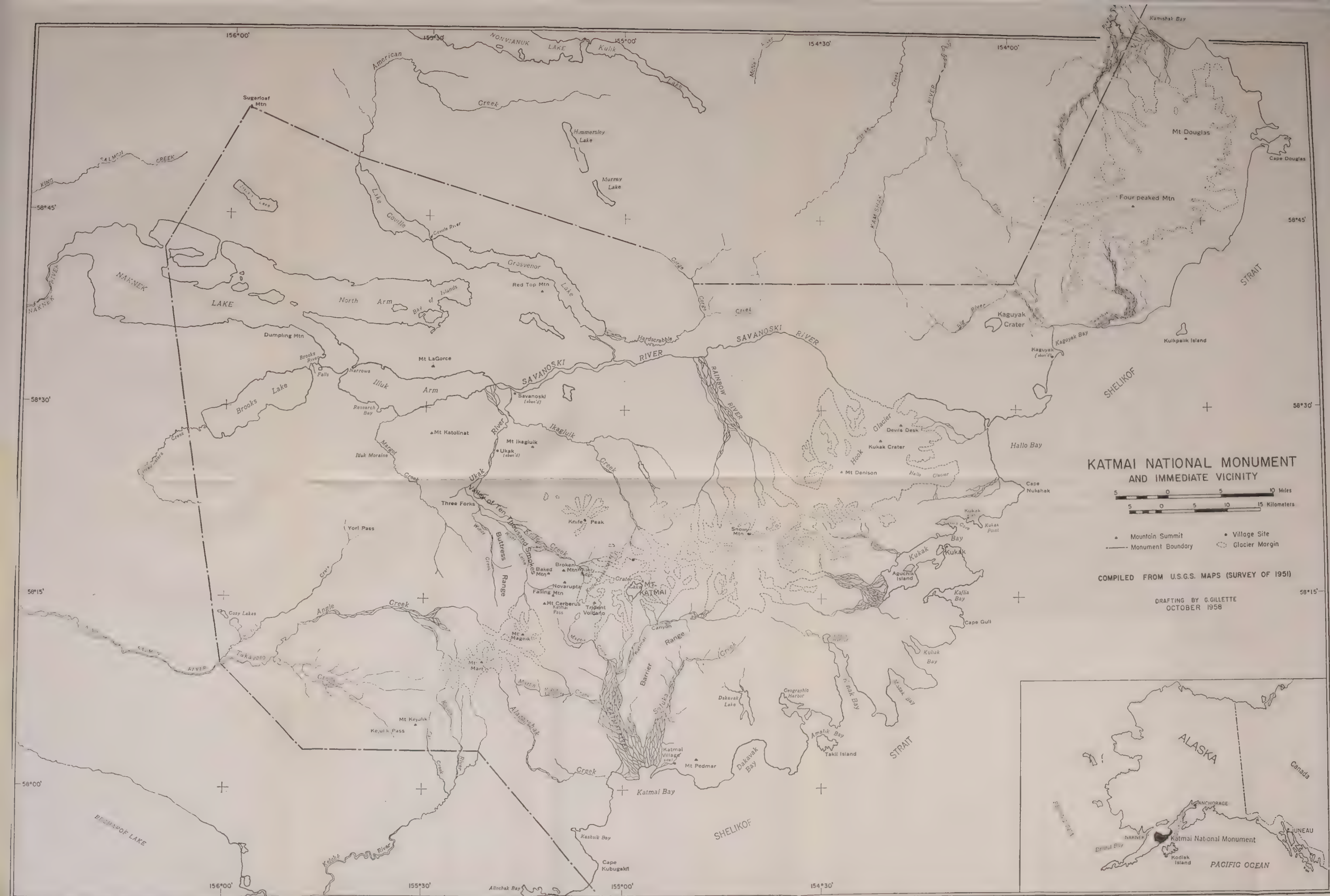


FIG. 4.—Map of Katmai National Monument, showing localities mentioned in the text.



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